CHAPTER THREE

Chondrus crispus – A Present and Historical Model Organism for Red Seaweeds

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Abstract

Chondrus crispus, or Irish moss, is a common edible red seaweed that can be found on rocky shores in the Northern Atlantic. The cell wall contains carrageenan and *C. crispus* is the original source of this commercially used thickener. Because of the ecological and economic importance of this red alga a relatively important research literature exists and one of the recent achievements in *C. crispus* research is the sequencing of its genome. In this chapter we review some of the literature with the aim to promote

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C. crispus as a model organism for florideophyte red seaweeds. We consider subjects like commercial and historical uses, ecology, genetics, population structure, mating systems, physiology, cell wall biology and genomics.

3.1 INTRODUCTION

The red algae are eukaryotic organisms without flagella and centrioles with floridean starch as their energy reserve, using chlorophyll *a* and with phycobiliproteins as accessory pigments, giving them their distinctive colour. There are around 6000 species of red algae described (Guiry, 2013) and most are multicellular, macroscopic, marine and have sexual reproduction. The red algae are one of the three groups forming the Archaeplastida, together with the glaucophytes and the green lineage, and are thought to have emerged as an independent lineage ~1500 million years ago (Yoon, Hackett, Ciniglia, Pinto, & Bhattacharya, 2004;Yoon, Müller, Sheath, Ott, & Bhattacharya, 2006).

Red seaweeds are important components of the inter- and subtidal flora and are commonly found where suitable substrates are available from the polar areas to the tropics and even though most species are marine, they also exist in brackish and freshwater (Woelkerling, 1990). Red algae are also economically important; over 9 million tonnes are cultivated annually (FAO, 2012), with a value of over 2000 million USD. Despite the importance of red algae, the number of researchers that dedicate themselves to their study is still deficient. We believe that one of the reasons for this lack of visibility of this interesting group of organisms is the absence of a model species.

Chondrus crispus is a red seaweed, also called Irish moss, belonging to the Florideophytes, a group of multicellular red algae comprising of 95% of extant species and most of the species with an ecological importance (Woelkerling, 1990). It exhibits dichotomous branching and can be up to 15 cm long (Figure 3.1). The colour varies from pale yellow, through green purplish red to almost black; in the gametophyte a blue iridescence can often be found. The morphology is very variable and numerous forms have been described (Chopin et al., 1996). It commonly occurs on rocky shores and other hard substrata, inter- and subtidally, in the North Atlantic (Provan & Maggs, 2012) and is a source of carrageenan. Because of the ecologic and economic interest in this species an important scientific literature exists compared to other seaweeds. In this chapter, we try to review some of the literature and promote its use as a model for florideophyte red algae. Some arguments for using *C. crispus* as a model are shown in Table 3.1.

Figure 3.1 *Chondrus crispus* Stackhouse Gigartinales and the family Gigartinaceae. *Photo by Jonas Collén.*

Table 3.1 Principal Arguments for Choosing ***Chondrus crispus*** as a Representative of the Red Macroalgae and of the Florideophytes

- Typical red seaweed – allows for generalisations to other red algae
- Well-defined species – simplifying ecological and physiological studies
- Complex multicellularity – allows for comparisons and basic studies
- Large morphological plasticity – allows for studies on correlation between morphology, environmental factors and genotype
- Well studied red alga – background knowledge available
- Common, ecologically important species – increases the importance of the research
- Relatively small genome (105 Mbp) – facilitates sequencing and genomic studies
- Easily cultivated in the laboratory – gives the possibility of controlled studies
- Three different life cycle phases, accessible in the laboratory and in the field – allows for studies on effects of ploidy
- Cell wall composed of carrageenan, with different types being produced in different life cycle stages
- Related to economically important species – can give insight into the biology of, for example, *Eucheuma* and *Kappaphycus* species
- Of commercial interest – increases the interest in applied research

3.2 HISTORY

Chondrus crispus or Irish moss has been collected and utilised for human activities for hundreds of years (Allen & Hatfield, 2004; Mouritsen, 2013; Thorbjarnarson, 1939), but it was only in the late eighteenth century that the alga was assigned a scientific name. It initially appeared as *Fucus filiformis* Hudson 1762 as well as *Fucus crispus* Linnaeus 1767 (Guiry, 2013; Taylor & Chen, 1973). Stackhouse, in 1797, determined that this taxon should be removed from the overly broad genus *Fucus* and entered Irish moss under the binomial *C. crispus* (Papenfuss, 1950). The species has long been recognised as being exceedingly polymorphic (Chopin et al., 1996), a fact that has resulted in a complicated synonomy (Newton, Devonald, & Jones, 1957). As early as 1797, Goodenough and Woodward, in their description of species for the Linnean Society added the comment regarding *F. crispus* that 'No plant can be supposed to vary more than this,' and to corroborate, Lamouroux in 1813 listed 8 varieties of the taxon, with 15 still undecided (Taylor & Chen, 1973).

Not surprisingly, the earliest references regarding the utilisation of *C. crispus* come from people living along the north eastern coastline of the Atlantic Ocean, where the alga has been collected for centuries as food and medicine (Allen & Hatfield, 2004). The properties of its major cell wall polysaccharides were noticed early by these people, and this characteristic ultimately resulted in the present day industrial utilisation of Irish moss. The first formal recognition of the gelling properties of boiled *F. crispus* were discovered by Turner (1809), and this mucilaginous matter was named carrageenin by Pereira (1840), p. 564. The gelatinous, hot water-soluble mucilage of *C. crispus* was first isolated by Schmidt (1844). Coincidentally, in the same year, Forchhammer reported on the high sulphur content of the ash from *C. crispus* (Buggeln & Craigie, 1973).

Numerous common or vernacular names for *C. crispus* appear in many languages, i.e. Breton, English, French, Gaelic, German, Icelandic, Portuguese, Scandinavian, Spanish, Japanese and others (Chopin, 1986). This fact further attests to the longstanding and widespread use of the alga in human activities. Names such as carageen, carrageen, carrragheen, carraigin, carrageen moss, carrageen rock moss and Irish moss, etc. refer to the alga *C. crispus*. The etymology of carrageen remains uncertain although the word can be dated to 1829 when it may have been introduced as a commercial marketing term; its derivation from a town place in County Waterford, Ireland has been rejected (Bliss, 1985; Mitchell & Guiry, 1983).

The domestic use of Irish moss was documented at least as early as 1809 (Bliss, 1985; Mitchell & Guiry, 1983). An 1829 reference to 'carrageen' or Irish moss alluded to its putative therapeutic properties (Mitchell & Guiry, 1983), and a traditional treatment in Ireland for chest and lung ailments used Irish moss boiled in water or milk, strained and drunk hot (Allen & Hatfield, 2004). The alga also was used to treat kidney ailments and burns. These medicinal applications were so valued that a recipe for preparing a demulcent from *C. crispus* 'for diseases of debility' was included in an early *Materia Medica* (Frazer, 1864). The relaxing effects of the extracted carrageenans on mucous membranes provided relief in tuberculosis, whooping cough, pneumonia, quinsy and for various gastrointestinal complaints. In his report regarding the potential for trade and development of new materials for commerce in Europe, carrageen or Irish rock moss was appraised as a feasible industrial commodity (Simmonds, 1854).

Irish immigrants apparently carried the knowledge of the folk uses of Irish moss to the Americans very early in the nineteenth century, many of who settled in Boston, Massachusetts. Their requirements for carrageen were met by importing the dried seaweed, which in the early 1830s sold for US$1–$2 per pound (Humm, 1951; Smith, 1905). Dr J. V. C. Smith, a former mayor of Boston, pointed out to citizens, in 1835, that the rocky Massachusetts coastline supported an abundance of Irish moss. Irish fishers, Daniel Ward and Miles O'Brien of Scituate, Massachusetts, appear to have initiated the first commercial harvesting of seaweed in the USA between 1848 and 1850 (www.stmaryscituate.org/aboutus_history.html).

Events relating to World War II provided a catalyst for the rejuvenation of the Irish moss industry. In particular, interdiction of the Asian sources of agar needed for bacteriology and penicillin production focussed attention on alternative domestic resources in both Europe and America. Relatively low biomass of agarophytes along North Atlantic coastlines meant carrageenophytes must be evaluated (Marshall, Newton, & Orr, 1949, 184 pp.). A process was developed and an agar substitute from Irish moss, termed 'British agar', was produced. It turned out to be quite suitable for bacteriological purposes, being superior in clarity to conventional agar.

By 1952, Irish moss extractives were second in volume of production (~1.75 million lbs/annum) to alginates in the USA, with food, drug and cosmetic and industrial applications consuming 50%, 40% and 10% of the moss extract respectively (Jertson, 1952). The first carload of Irish moss shipped from Canada was from Nova Scotia (10,000 lb in 1940) with a

Newfoundland harvest of 28,795 lb in 1941. Exports from Prince Edward Island began in 1941with the shipping of 208,000 lb of dry moss (Humm, 1951). Irish moss harvesting in the Canadian Maritimes increased from 1.49 million lbs in 1943 to 87.05 million lbs in 1968 with the most rapid increase occurring after 1965 (Snaith, MacFarlane, & Johnston, 1969).

The annual standing crop of *C. crispus* is often variable and the labour associated with hand harvesting is arduous, and eventually commercial harvesting in Europe gave way to smaller, localised enterprises (Guiry & Hession, 1998). In North America, drag-rake harvesting became common practice by the mid-1950s, but the dramatic increase in Irish moss landings in the Canadian Maritimes during the late 1960s (Ffrench, 1971; Pringle & Mathieson, 1987; Snaith et al., 1969) was considered unsustainable. Implementing modern farming technologies was then suggested as a means of supplementing the natural harvest (Neish, 1968; Neish & Fox, 1971). In 1972, the first pilot-scale cultivation trials were conducted in Nova Scotia at Meteghan and in New Brunswick at Point Sapin. Two commercial firms, Genu Products Canada Limited and Marine Colloids Inc., of Rockland, Maine (Craigie & Shacklock, 1989; Mathieson, 1982) were involved. Early stage *C. crispus* cultivation facilities appeared in France in 1976, and together, these clearly demonstrated proof of concept for growing Irish moss in tanks on land (Braud, 2006; Craigie, 1990; Craigie & Shacklock, 1989; Mathieson, 1982). One, Acadian Seaplants Limited, Charlesville, is in commercial operation today.

Cultivated *Eucheuma* spp. from the Philippines began to enter the carrageenophyte market in significant quantities in the mid-1970s (Ricohermoso & Deveau, 1979) resulting in a dramatic reduction in demand for the more expensive Canadian Irish moss, which, until 1975, had supplied 75% of the world's raw material for carrageenan production (Pringle & Mathieson, 1987). The worldwide shortage of carrageenophytes in the 1970s led to similar collaborations between science and industry in France and focus on cultivating *C. crispus* in tanks intensified (Braud, 2006; Braud & Delépine, 1981). Cultivation of Irish moss in the sea also was considered independently in Canada and in France by SATIA, but the cost of such farmed seaweed precluded further development (Briand, 1991; Chopin, Sharp, Belyea, Semple, & Jones, 1999; DeRoeck-Holtzhauer, 1991). Although cultivated Irish moss was now uncompetitive as a carrageenan source, the Marine Colloids Inc. technology and infrastructure for cultivating this species was acquired in 1981 by Acadian Seaplants Ltd and by the early 1990s Irish moss was used directly as a food.

3.3 ECOLOGY

Chondrus crispus is considered as a cold water and euryhaline species that inhabits the intertidal zone and is usually most abundant at 4–7 m below mean low water (MLW) but may extend from −18 m to more than +1 m and has been dredged from depths of −38 m MLW (Mathieson & Burns, 1975). The lower limits of vertical distribution are probably determined by a variety of factors such as wave action, water transparency, availability of solid substrata and competition for space. *Chondrus crispus* can be found growing on rocks in lower intertidal and shallow subtidal zones or in pools in the mid-intertidal zone in exposed locations. The most extensive populations occur on massive horizontal boulders on semi-exposed and open coastal sites, with reduced populations on smaller rocks and sand or sediment-covered rocks. Occasionally, *C. crispus* occur as detached healthy floating populations in the sublittoral zone (Prince & Kingsbury 1973a). The extensive distribution in estuarine habitats suggests a broad tolerance to temperature, salinity and light (Mathieson & Burns, 1971; Mathieson & Prince, 1973). On European coasts only a few plants occur as fixed forms at more than 20 m depth, while on the Canadian coasts, there are extensive settlements at this depth, indicating some differences in the potential of the species in these two regions (Kopp & Perez, 1978).

Chondrus crispus can be found in various forms that range from sporadic patches of thalli arising from a single holdfast to areas where the substratum is covered with a dense, uniform canopy (with numerous stipes per cm^2) on intertidal and shallow subtidal rocky shores (Johnson, 2001). In comparison with solitary thalli, dense canopies are known to offer protection against flow-induced mechanical forces (Johnson, 2001) and thus increasing productivity and growth. It can also form dense patches beneath *Fucus* or beneath canopy-forming kelps such as *Laminaria digitata* (Schaal, Riera, & Leroux, 2010).

Chondrus crispus is widely distributed in the north western and north eastern Atlantic and adjacent waters, such as the North Sea. In the western Atlantic *C. crispus* is found from Labrador to New Jersey and in the Eastern Atlantic from approximately 69° N in Norway and on the southern coasts of Iceland to Portugal (MacFarlane, 1968; Provan & Maggs, 2012). Some sources mention records of *C. crispus* from California to Japan, however, any distribution outside the Northern Atlantic needs to be verified and probably results from confusion with other species of the same genus in the Pacific Ocean (Hu, Guiry, Critchley, & Duan, 2010).

In the Atlantic only one species of *Chondrus* is known – *C. crispus*, but other species exist in the Pacific Ocean: *Chondrus ocellatus* Holmes, *Chondrus giganteus* Yendo, *Chondrus nipponicus* Yendo, *Chondrus yendoi* Yamada & Mikami, *Chondrus pinnulatus* (Harvey) Okamura, *Chondrus armatus* (Harvey) Okamura, *Chondrus verrucosus* Mikami and *Chondrus retortus* Matsumoto & Shimada. *Chondrus giganteus* can also be found in Mediterranean as an introduced species (Hu et al., 2007; Matsumoto & Shimada, 2013).

The current geographical distribution of *C. crispus* is primarily determined by temperatures and consequently it may be impacted by global change and increasing water temperatures. For instance, Lima, Ribeiro, Queiroz, Hawkins, and Santos (2007) reported a northward shift of *C. crispus* from the southern limit of Portuguese populations of 180 km since 1971. In addition, a study using temperature-controlled water baths, Lüning, Guiry, and Masuda (1986) showed that most European strains of *C. crispus* ranging from northern Norway and Iceland to northern Spain survived a uniform upper temperature limit of 28 °C with a few European strains from the North Sea and English Channel area being able to sustain a 29 °C limit. Temperature has also a drastic effect on the reproduction of the species, Prince and Kingsbury (1973b) showed that the optimum temperature for germination and growth of spores (carpospores and tetraspores) was 21 °C. At temperatures above this threshold, spores died or developed abnormally after a few days of exposure. Above 30 °C even brief shock treatments result in spore mortality. At the other extreme, cultures maintained at 4 °C displayed inhibition of germination and growth.

Natural populations of *C. crispus* can survive freezing temperatures, but repeated freezing exposures can significantly limit productivity and biomass and thus influence the competitive ability of the species. Dudgeon, Davison, and Vadas (1990) showed that chronic freezing temperatures combined with high irradiance induced bleaching and fragmentation of fronds. Holdfasts survived the exposure and were capable of regenerating. The authors postulated that *C. crispus* combats freezing stress by phenotypic acclimation through maintenance of photosynthesis rather than by genetic adaptation.

3.4 LIFE CYCLE

The sexual life history of *C. crispus* was described by Darbishire in 1902. Nonmotile, short-lived male gametes (spermatia) are released and fertilise an egg (carpogonium) retained on the female gametophyte. The zygote is mitotically amplified within the cystocarp, a structure also

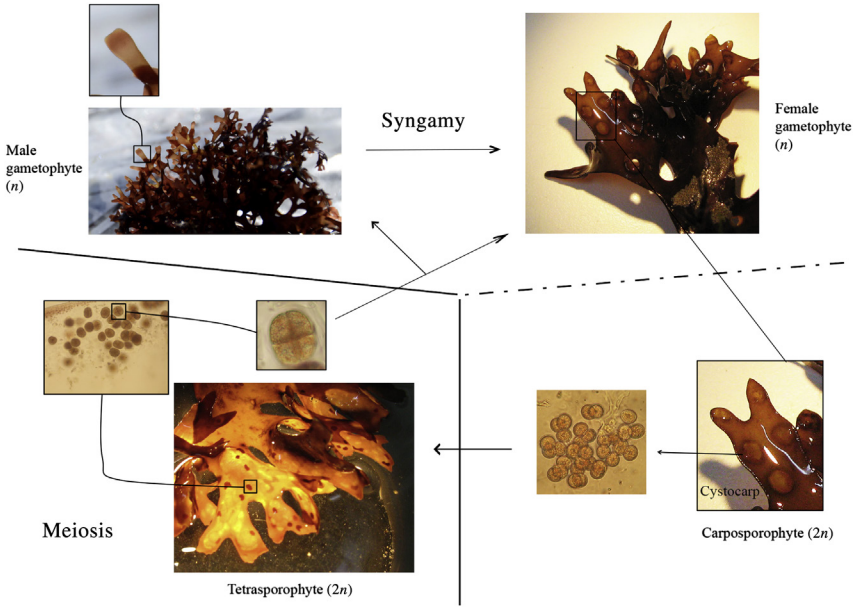

Figure 3.2 The life cycle of *Chondrus crispus*. A nonmotile spermatium fertilises the carpogonium which is retained on the female gametophytic thallus (*syngamy*). Within the cystocarp, the zygote is mitotically amplified potentially liberating thousands of genetically identical diploid carpospores following a single fertilisation event. The diploid carpospores produce the diploid free-living tetrasporophyte. *Meiosis* occurs in the tetrasporophyte, releasing haploid tetraspores which form the free-living female and male gametophytes. (See the colour plate.) *Images: S.A. Krueger-Hadfield.*

retained on the female thallus. The resulting diploid carpospores are an additional dispersive stage in comparison to other algal life cycles and germinate into the free-living tetrasporophyte. The tetrasporophyte produces haploid tetraspores via meiosis, which germinate into gametophytes (Figure 3.2).

Chen and McLachlan (1972) observed an increase in the number of cystocarps produced when male and female gametophytes obtained from cultured tetraspores were crossed in aerated culture chambers. Moreover, cystocarps failed to develop in the absence of male gametophytes, providing presumptive evidence of fertilisation (Chen & McLachlan, 1972). Krueger-Hadfield, Roze, Destombe, Correa, and Valero (2014) were the first to demonstrate cross fertilisation using genetic markers in the field and in the laboratory.

Male gametophytic fronds tend to be narrower, bearing spermatangial sori near the apices, which appear as pink or white bands (Darbishire, 1902;

Taylor & Chen, 1973; Tveter-Gallgher, Mathieson, & Cheney, 1980). The white bands on reproductive males are distinct and located 3–10 mm below the apex, whereas, actively growing apices are pale tan or white only at the apex (Krueger-Hadfield, 2011). After spermatial discharge, the thalli disintegrate at the point immediately below the sori (Chen & McLachlan, 1972).

Female gametophytic fronds are slightly wider at the apices and, when fertile, bear distinctive cystocarpic tissue (Chen & McLachlan, 1972). Fredericq, Brodie, and Hommersand (1992) found female gametophytes bearing cystocarps, which contained small patches of elongate surface cells near the apex which appeared to function as spermatangial initial cells. However, paternity analyses in natural populations of *C. crispus* revealed the presence of male alleles in cystocarpic DNA, with the exception of 11 cystocarps (<2%) that only exhibited one allele at all microsatellite loci (Krueger-Hadfield et al., 2014).

Tetrasporophytic fronds have broad apices similar to female gametophytes. When fertile, the apices are covered in ovate tetrasporangial sori, which appear reddish-orange in colour and bulge slightly from both surfaces of the frond (Taylor & Chen, 1973). Once the sori have released the tetraspores, the apical tissue appears a lighter colour than the remainder of the frond.

3.5 GENETICS, POPULATION STRUCTURE AND THE MATING SYSTEM

Mendelian genetic analyses were an excellent tool for studying inheritance patterns before molecular genetic tools were readily available. van der Meer (1987) reviewed the use of colour mutants to detect fertilisation, distinguish between self- and cross fertilisation and to distinguish between sexual and asexual processes. Pigmentation mutants of *C. crispus* were found to either follow strict maternal inheritance or classic Mendelian transmission ratios, for example, cell masses in old tetrasporangial sori found in culture were the product of an asexual process in somatic tetrasporangial tissue (van der Meer, 1987). None of the studies using molecular genetic markers (e.g. Cheney & Mathieson, 1979; Chopin et al., 1996; Donaldson, Chopin, & Saunders, 2000) were sufficiently powerful in order to explore the mating system and gene flow in detail. This is all the more surprising as the majority of populations are gametophyte biased, male gametophytes were thought to be rare (but see Krueger-Hadfield, Roze, Mauger, & Valero, 2013; Tveter-Gallagher et al., 1980) and genet identification is virtually impossible

when holdfasts form contiguous mats on the available substrata and give rise to numerous upright fronds (Bhattacharya, 1985). Moreover, coalescence of neighbouring genets may occur in the field, resulting in chimeric holdfasts that consist of more than one genotype (Krueger-Hadfield, 2011; Santelices et al., 1999; Scrosati & Mudge, 2004; Tveter-Gallagher & Mathieson, 1980).

Using different markers, such as isozymes (Cheney & Mathieson, 1979), restriction fragment length polymorphism (Chopin et al., 1996), amplified fragment length polymorphism (Donaldson et al., 2000) and inter-simple sequence repeat (Wang et al., 2008), *C. crispus* has been found to be highly genetically variable over its range distribution. These molecular markers were analysed at large geographic scales establishing that *C. crispus* on both sides of the North Atlantic are conspecific (Chopin et al., 1996) as well as indicating limited dispersal capacities (Donaldson et al., 2000; Wang et al., 2008; Provan & Maggs, 2012). There were, however, discrepancies among the studies regarding the relationship between gene flow and geographic distance (Donaldson et al., 2000; Hu et al., 2010; Provan, Glendinning, Kelly, & Maggs, 2013; Wang et al., 2008).

Krueger-Hadfield, Collén, Daguin–Thiébaut, and Valero (2011) were the first study to directly assess genetic structure and the mating system in *C. crispus* using codominant microsatellite loci. The authors found very few repeated multilocus genotypes, no difference in allele frequencies between haploid and diploid phases and no linkage disequilibrium, suggesting sexual reproduction was the prevailing reproductive mode. Moreover, there was no detectable cystocarpic effect as the tetrasporophytes sampled had unique multilocus genotypes. However, it was not possible to distinguish between high levels of inbreeding or spatial substructuring in driving the significant pattern of heterozygote deficiency. In order to effectively address this issue, Krueger-Hadfield et al., (2013) explored hierarchical population structure at high and low shore populations and demonstrated heterozygote deficiencies were driven by high levels of inbreeding. Second, high and low shore individuals were found to belong to genetically differentiated populations, despite being separated by less than a few meters in vertical tidal height and less than 30 m in horizontal topographical distance. Third, gene flow was restricted within the high shore habitat due to daily tidal cycles where the high shore population could be exposed for twice the amount of time as the low shore population. Within-shore genetic differentiation reduced genetic diversity and increased levels of inbreeding indicated the high shore as a marginal environment. The results from Krueger-Hadfield et al. (2011, 2013) suggested the same mechanisms as those occurring over a species'

distributional range may be at work at fine scales within the intertidal shorescape with core and marginal population dynamics.

Yet, indirect estimates of the mating system (i.e. F_{is}) can be strongly influenced by spatial substructuring or biparental inbreeding (i.e. mating between close relatives). Paternity analyses have been used to describe the mating system of animals and plants (e.g. Zipperle, Coyer, Reise, Stam, & Olsen, 2011), but have rarely been applied to red seaweeds (but see, Engel, Wattierf, Destombe, & Valero, 1999). Moreover, paternity analyses enable the detection of apomixis or intragametophytic selfing (i.e. the fusion of gametes produced by the same gametophyte, resulting in homozygosity at all loci, Klekowski, 1973), which would otherwise be difficult to detect by only analysing population structure. Krueger-Hadfield et al. (2014) documented higher levels of relatedness between males siring carpogonia on a single female gametophyte than when compared to males in the entire population. Moreover, the paternity analyses verified hypotheses of restricted spermatial and clumped spore dispersal generating high levels of inbreeding as proposed in Krueger-Hadfield et al. (2013).

In order to understand the impacts of the intertidal shorescape on gene flow and the mating system in *C. crispus*, the first hurdle is the identification of a genet. The majority of studies have utilised different sampling techniques in which the genet (holdfast including all upright fronds; *sensu* Kautsky & Ehn, 1993) or the ramet (frond; e.g. Bhattacharya, 1985) was studied. Krueger-Hadfield (2011) sampled each frond from two morphologically distinct gametophytic holdfasts grown in the laboratory from tetraspores. At least six different genotypes were detected among the two holdfasts, suggesting holdfasts in the field may be composed of more than one genotype. Moreover, in natural populations, holdfasts of mixed ploidy are common (Plumb, 1999; S. A. Krueger-Hadfield, pers. obs.). By understanding genet composition and distribution within the shore, it will be possible to determine spermatial and spore dispersal distance and describe gene flow in more detail.

3.6 ECOLOGICAL AND BIOCHEMICAL ASPECTS OF BIOTIC INTERACTIONS

Field observations of biotic interactions with smaller organisms are rather limited for *C. crispus* (Andrews, 1976; Krueger-Hadfield, 2011), but it can be heavily fouled by epibionts, such as ascidians and bryozoans (Wahl & Mark, 1999) and this is strongly dependent of interactions with snails

(Stachowicz & Whitlatch, 2005). No adelphoparasite or unpigmented red algal parasite is known in *C. crispus* (Goff, 1982). However, as early as 1889, the ascomycete *Lautitia danica* was described growing on the cystocarps of *C. crispus* by Rostrup (1889) in Denmark and later more detailed studies were provided (Jones, 1898; Rosenvinge, 1906). The fungus was present all year round in cystocarps but also in tetrasporangia (Stanley, 1992; Wilson & Knoyle, 1961). In natural populations, *C. crispus* is also plagued with a variety of green (*Acrochaete* spp., *Phaeophila dendroides*) and brown (*Streblonema* spp.) algal endophytes, as well as with the oomycete *Petersenia pollagaster* (reviewed in Correa, 1996).

Surprisingly, knowledge on *C. crispus*-associated bacteria is limited as a description of surface fouling (Sieburth & Tootle, 1981). This limited knowledge may be related to the fact that the species is known to shed outer layers of cell wall and cuticle glycoproteins to clean its surface from epibionts (Craigie, Correa, & Gordon, 1992; Correa & McLachlan, 1988).

A better knowledge during the 1980s and 1990s corresponded to the establishment of large-scale cultivation farms of *C. crispus* with increased frequency of pathologies (Craigie & Correa, 1996). These authors described the etiology of a number of infection diseases in cultivated *C. crispus* from Canada. Grazer impacts were also shown to be heavy in these land-based cultivation systems at early stages. Schacklock and Croft (1981) described important damage and differential effects caused by isopod, amphipod and gastropod grazers in maricultured *C. crispus*. The main frequent epiphytes in tank cultures of *C. crispus* are *Ulva* spp. and members of the brown algae Ectocarpales and, interestingly, it was proposed to introduce some amphipod grazers in culture tanks to keep the thallus clean of epiphytes (Schacklock & Doyle, 1983).

One of the most important diseases resulting in tissue degradation was reported to be caused by the oomycete *Petersenia pollagaster* (Craigie & Shacklock, 1989; Molina, Hughes, & Craigie, 1988). The parasite selectively destroys frond apices. But studies of biotic interactions culminated with the in-depth studies of endophytism by small filamentous green algae in natural and cultivated populations of *C. crispus* in Atlantic Canada (Correa & McLachlan, 1991, 1992, 1994; Correa, Nielsen, & Grund, 1988; Nielsen & McLachlan, 1986; Correa et al., 1987). Of particular interest is its association with *Acrochaete operculata*, as it displays a high degree of host-phase specificity (Correa & McLachlan, 1991). The filaments of the green alga are able to completely invade the medullary tissues of the sporophytic generation of the red alga, whereas they do not penetrate beyond the outer cell layers of the

gametophytic plants (Correa & McLachlan, 1991, 1994). In consequence, it causes cellular damage only to the sporophytes of *C. crispus* (Rhodophyta) and leads to secondary bacterial infections by facultative pathogens from the *Cytophaga/Flavobacterium* group (Correa & McLachlan, 1992; Craigie & Correa, 1996). In addition, these sporophytes are more palatable for isopod grazers (Correa & McLachlan, 1992). This evidence suggested that host specificity in *A. operculata* is determined by cell wall composition of the hosts, likely the carrageenan fraction. In contrast, *Acrochaete heteroclada* was not host specific, infecting all offered hosts, including carrageenophytes and agarophytes (Correa & McLachlan, 1991). This hypothesis of host recognition through the perception of cell wall galactans was later tested and validated by Bouarab, Potin, Correa, and Kloareg (1999). The life cycle phases of *C. crispus* differ by the degree of sulphation of their cell wall carrageenans. The preincubation of *A. operculata* zoospores with κ-type oligocarrageenans, only present in the gametophyte cell walls, was shown to significantly decrease the penetration of *A. operculata* into *C. crispus* sporophytic tissues, whereas the elicitation by sporophyte-specific λ oligocarrageenans increases its virulence against *C. crispus* gametophytes (Bouarab et al., 1999).

In *C. crispus*, the investigations of metabolic regulations during this specific interaction have contributed to a better knowledge of the immunity responses of red algae. (For reviews Bouarab, Kloareg, Potin, & Correa, 2001; Bouarab, Potin, Weinberger, Correa, & Kloareg, 2001; Cosse, Leblanc, & Potin, 2008; Potin, 2008; Weinberger & Potin, 2010). *Chondrus crispus* gametophytes respond to cell-free extract of *A. operculata*, by the emission of reactive oxygen species essential in gametophyte resistance and through the activation of a NADPH oxidase homolog (Bouarab et al., 1999). This enzyme is likely to be encoded by the homolog of respiratory burst oxidase $gp91^{phox}$, later characterised in *C. crispus* (Hervé, Tonon, Collén, Corre, & Boyen, 2006). The induced resistance of gametophytes was shown to be dependent of the downstream activation of signalling cascades involving compounds derived from the oxidative metabolism of polyunsaturated fatty acids (PUFAs) (Bouarab et al., 2004). It was the first demonstration that the oxylipin pathways are activated during immunity responses of red algae (Bouarab et al., 2004). In this context, the methyl ester of the plant stress hormone jasmonic acid was revealed to promote the liberation of both C20 and C18 PUFAs-derivative oxylipins, such as prostaglandins, and to increase transcription of defence-related genes (Gaquerel et al., 2007; Hervé et al., 2006). Contact of *A. operculata* with κ-oligocarrageenans also enhances secretion of L-asparagine, which in turn induces a release of H_2O_2

by *C. crispus* (Weinberger, Pohnert, Kloareg, & Potin, 2002). This reaction is apparently catalysed by an apoplastic L-amino acid oxidoreductase and could prevent settlement of *A. operculata* zoospores (Weinberger et al., 2005). The gametophytes also synthesise ultraviolet absorbing compounds around the sites of *A. operculata* zoospore penetration. This reaction suggests the involvement of the phenylpropanoid metabolism, as also shown by the activation of shikimate dehydrogenase and phenylalanine ammonialyase (Bouarab et al., 2004). The emission of volatile halocarbon compounds is another chemical defence strategy used by *C. crispus*, as shown in other red algae (for reviews Potin, Bouarab, Salaün, Pohnert, & Kloareg, 2002; Weinberger & Potin, 2010).

Biotic interactions are not solely negatively affecting *C. crispus.* Positive interactions were shown to occur in raceway tanks between the diatom *Odontella aurita* and *C. crispus* as well as the edible red alga *Palmaria palmata*. Allelopathic compounds or other exudates emitted by the two species favour diatom aquaculture and prevent the contamination of these cultures by other microalgal species that often bloom in pond cultivation (Braud, 1998).

3.7 PHOTOSYNTHESIS

Chondrus crispus has a relatively important research history concerning its photosynthesis due to its abundance and its suitability for measurements of physiological parameters. This literature dates back to at least 1885 (Rattray, 1886) where it was noted that photosynthesis of *C. crispus* was relatively low in November. Intertidal algae are exposed to varying light regimes with seasons, weather patterns, diurnal changes and tidal cycles and need to be able to acclimate or adapt in order to react to the patterns of immersion and emersion and associated changes in light, temperature, pH, CO_2-content and osmolarity. A number of studies have highlighted the importance of these environmental parameters on the photosynthesis of *C. crispus*.

Light and temperature are key factors regulating photosynthesis. Maximum photosynthesis of *C. crispus* is typically found around 200 µmol photons/m^2/s (Brechignac & Andre, 1984b; Johansson & Snoeijs, 2002; Mathieson & Norall, 1975) with photoinhibition occurring at higher light intensities (Mathieson & Burns, 1971). Algae collected subtidally had maximum photosynthetic rate at lower light intensities and tetrasporophytes exhibited higher photosynthetic rates than female gametophytes (Mathieson & Norall, 1975). Optimum temperatures for photosynthesis have been reported between 20

and 25 °C (Kübler & Davison, 1993; Mathieson & Burns, 1971). This range is higher than is usually indicated as optimal for growth, 6–18 °C (Bidwell, McLachlan, & Lloyd, 1985). The efficiency of photosynthesis has been shown to decrease at noon and increase in the late afternoon (Sagert, Forster, Feuerpfeil, & Schubert, 1997).

One aspect of light and photosynthesis that has attracted much attention is the effect of UV-radiation. There is important literature on effects on thalli (e.g. Bischof et al., 2007; Kräbs & Wiencke, 2005; Roleda, Wiencke, Hanelt, & Bischof, 2007; and references therein). In intertidal algae living in northern temperate and polar regions, freezing is an extreme form of temperature stress and affects *C. crispus* in the northern part of its range. Twelve hours of freezing at −20 °C caused a decrease in photosynthesis by 58% and a decrease in respiration by 32% with a concomitant efflux of amino acids, indicating membrane damage (Davison, Dudgeon, & Ruan, 1989). *Chondrus crispus* showed full recovery of photosynthesis, 48 h after 3 h exposure to −20 °C, whereas, after 6 h at −20 °C, full recovery was not seen (Dudgeon, Davison, & Vadas, 1989). The freezing causes tissue freezing (Davison et al., 1989; Kanwisher, 1957). The effects of freezing can be reduced by acclimation; daily freezing at −5 °C reduced the photosynthesis initially with 75%, but after acclimation to subsequent freezing, photosynthesis decreased only by 40% (Dudgeon et al., 1990). The acclimation to freezing also reduced the release of amino acids after exposure.

In order to achieve efficient photosynthesis, internal concentrations of CO_2 need to be sufficient to reduce photorespiration. Carbon concentration mechanisms have been demonstrated in many seaweeds (Raven & Hurd, 2012) including *C. crispus* (Bréchignac et al., 1985a, Brechignac, Andre, & Gerbaud, 1986). Thallus and protoplasts of *C. crispus* use extracellular and intracellular carbonic anhydrase to increase the availability of CO_2 for Rubisco (Smith & Bidwell, 1987, 1989a) while the direct use of HCO_3^- remains unclear. Brechignac et al. (1986) suggested it to be important, while Smith & Bidwell (1989b) showed different results. *Chondrus crispus* does not seem to be limited by content of inorganic carbon since increased growth with increased CO_2 was only seen at high temperatures (Sarker, Bartsch, Olischläger, Gutow, & Wiencke, 2013). It should also be noted that *C. crispus* lacks pyrenoids, chloroplast Rubisco-containing bodies, which have a role in carbon concentrating mechanisms (Badger et al., 1998).

Photosynthetic organisms need systems to control the efficiency of their photosynthetic apparatus as well as balancing the energy between photosystem 1 and 2 (PS1 and PS2). In *C. crispus,* this is achieved by a spill-over from

PS1 to PS2, which is a direct funnelling of energy from PS1 to PS2 without going through the reaction centre of PS1. This process is controlled by the redox status of the plastoquinone pool (Kowalczyk et al., 2013).

In addition to oxygen production, during daytime, oxygen uptake during photosynthesis has been studied in *C. crispus* in some detail (Brechignac & Andre, 1984, 1985b; Brechignac & Furbank, 1987). The oxygen uptake represents 37% of the net photosynthesis and was always higher than dark respiration. During CO_2 limiting conditions, Rubisco oxygenase activity represented less than half of oxygen uptake, pseudocyclic photophosporylation less than 20% and other reactions, such as respiration, the remainder. These studies showed that the uptake of oxygen in the light was relatively insensitive to CO_2 concentrations, but sensitive to increased oxygen concentrations.

3.8 GENES AND GENOMES

A crucial element for the establishment of a biological model organism is an important and pertinent knowledge of the genes and genomes of the organism. This enables the use of high throughput molecular methods and for global comparisons with other organisms. Presently, the knowledge of genes and genomes in *C. crispus* is more important than in other red macroalgae allowing for its efficient use in scientific research. To our knowledge the first genome sequence from *C. crispus*, of the 18S rRNA gene dates to 1992 (Bird, Murphy, Rice, & Ragan, 1992), even though the amino acid sequence of flavodoxin was known earlier, analysed through enzymatic digestion of the protein (Wakabayashi, Kimura, Fukuyama, Matsubara, & Rogers, 1989).

The mitochondrial genes and genome of *C. crispus* have been sequenced and studied (Boyen, Leblanc, Bonnard, Rienenberger, & Kloareg, 1994; Boyen, Leblanc, Kloareg, & Loiseaux-de Goer, 1994; Leblanc, Boyen, et al., 1995; Leblanc, Kloareg, Loiseaux-de Goër, & Boyen, 1995; Leblanc et al., 1997; Richard, Bonnard, Grienenberger, Kloareg, & Boyen, 1998; Richard, Kloareg, & Boyen, 1999; Viehmann, Richard, Boyen, & Zetsche, 1996). The mitochondrial genome is circular and has a relatively small size (26 kb), and is thus very different from angiosperms, despite the fact that the genes are phylogenetically close. It codes for 51 genes, has high coding density (95.2% coding) with only one intron and contains ten overlapping regions. The genome is transcribed into two large primary transcripts that are further matured via multiple processing steps involving tRNA genes.

The plastid genome of *C. crispus* was sequenced as a part of the genome project. The relatively large of size 180,086 bp is typical for most red algae. The genome codes for 240 unique genes of which 204 are protein coding and three genes are of unknown function (Janouškovec et al., 2013). One unprecedented feature found in *C. crispus* and other florideophyte red algae is a group II intron in a tRNA-Met gene that encodes a maturase.

The nuclear genome of *C. crispus* is 105 Mbp, is estimated to code for 9606 genes (Collén et al., 2013). The genes are characterised by their compact nature, caused by the very low content of introns considering the genome size and small untranslated regions (UTR) (Figure 3.3). 88% of genes have no introns and the existing introns are typically short with an average length of only 182 bp. Taken together this means that the genome is by dominated intergenetic DNA, with a high degree of repetition. The intergenetic DNA is organised in regions with low gene density interspersed with clusters of genes with short distances between protein coding genes and with very high gene density. The low intron content, small UTR and clustered genes are generally associated with compact small genomes. This resemblance with compact genomes is also seen by the relatively low number of genes, the small genome families and with no indication of genome duplication.

Prior to the genome project a study was performed in order to gain increased knowledge of genes in red algae and in particular genes important for cell wall synthesis (Collén et al., 2006b). The study compared the transcriptome of protoplasts (cells devoid of cell wall after treatment with cell wall digesting enzymes) and nonstressed thallus plants. The approach yielded 2291 nonredundant sequences with a large repertoire of stress genes as well as many genes of unknown function. The collection of expressed

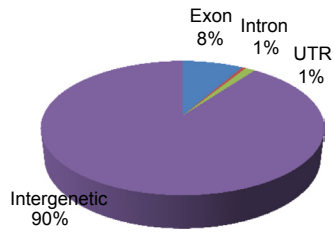

Figure 3.3 Genome composition of *Chondrus crispus*. The intergenetic part of the genome is the nonprotein coding parts between genes and the UTR are the 5′ and 3′ nontranslated part of the genes. UTR, untranslated regions.

sequence tags (ESTs) were also used to construct cDNA microarrays that were subsequently used for physiological studies (Collén et al., 2006a; Collén, Guisle–Marsollier, Léger, & Boyen, 2007). To support the annotation in the genome project another 300,000 ESTs were sequenced representing 8212 contigs (Collén et al., 2013).

3.9 PERSPECTIVES ON PRIMARY METABOLISM

Most of the primary amino acid metabolic related genes were found in single copy in the *C. crispus* genome, with the exception of glutamine synthase, aspartate transaminase and urea transporters (Collén et al., 2013). *Chondrus crispus* lacks the glutamate synthase gene, thus glutamate would necessarily be synthesised by glutamate dehydrogenase and not through the cleavage of glutamine by glutamate synthase. The genome appears to contain no ureases or arginases, important for the urea cycle, though it does have genes coding for urea transporters. It is likely that *C. crispus* can metabolise urea as a gene encoding a fusion protein of urea carboxylase and allophanate hydrolase was identified and degradation of urea by such fusion proteins has previously been shown (Genbauffe & Cooper, 1991). Due to the lack of arginases it is unlikely that proline is synthesised from arginine; however, the genome contains genes for a pyrroline-5-carboxylate reductase and a 1-pyrroline-5-carboxylate synthase suggesting that *C. crispus* is capable of synthesising proline from glutamate. For UV protection *C. crispus* synthesises the UV-absorbing mycosporine-like amino acid shinorine (Kräbs, Watanabe, & Wiencke, 2004). Other amino acids identified include gigartinine, L-citrullinyl-L-arginine, ornithine and citrulline (Laycock & Craigie, 1977; Young & Smith, 1958).

The *C. crispus* genome codes for all enzymes involved in plastidial fatty acid synthesis and their transport to the cytosol. Furthermore, it has at least one gene for each of the enzymes involved in the microsomal fatty acid elongase complex. It produces PUFAs and is notable for its high levels of arachidonic acid (Fleurence, Gutbier, Mabeau, & Leray, 1994; van Ginneken, Helsper, de Visser, van Keulen, & Brandenburg, 2011; Lamberto & Ackman, 1994). It is unlikely that fatty acid desaturation occurs in the plastid as the genome lacks an ACP desaturase although several potential desaturases have been annotated, comprising a stearyol-CoA desaturase, a Δ12 and a Δ15-desaturase and two genes for PUFA desaturases. Sphingolipids containing inositol that have been reported in other red algae (Khotimchenko, Klochkova, & Vaskovsky, 1990) and *C. crispus* shows the presence of genes required for

the production of 4-hydroxysphinganine, sphingosine-1-phosphate and ceramides, together with several genes for ceramide glycosyltransferases. A full complement of genes for the synthesis of thylakoid membrane lipids and phospholipids is contained within the genome. In addition, fatty acids may be stored in triacylglycerols through the acyl-CoA dependent or independent pathway. Free C18 and C20 fatty acids may be further processed into oxylipins.

Unlike plants and green algae, which store their insoluble starch granules in their chloroplasts, the carbon energy of red algae is stored in the cytosol as floridean starch (Viola, Nyvall, & Pedersen, 2001). The glycosyl transferase (GT) families 5 and 13, involved in starch synthesis and glycoside hydrolase (GH) families 13, 14, 35 and 77, involved in starch recycling, are encoded within the *C. crispus* genome. While this organism has all the required proteins for starch synthesis and breakdown, their corresponding genes are unexpectedly low in redundancy, demonstrating a system simpler than that found in the green lineage. Four genes have been identified for synthesis and one for degradation of trehalose, a nonreducing disaccharide. In plants, trehalose is important in starch and sucrose regulation; however, sucrose metabolism is lacking in *C. crispus* and thus trehalose may have a different biological role. Another low molecular weight carbohydrate is the photo-assimilate mannosylglycerate (digeneaside; 2-D-glycerate-α-D-mannopyranoside) found in some red algae, though it has not been detected in *C. crispus*. However, the genome holds a gene coding for a mannosylglycerate synthase (GT78), which was likely acquired in red algae by horizontal gene transfer from a thermophilic marine bacterium. An alternative hypothesis is that the GT78 in *C. crispus* may be involved in the synthesis of floridoside (2-0-D-glycerol-a-o-galactopyranoside) or isofloridoside (1-0-D-glycerol-a-D-galactopyranoside), two heterosides known to be accumulated in this alga (Kremer, 1980). One of the best characterised enzymes produced by *C. crispus* corresponds to a hexose oxidase which may be involved in algal defence and which oxidises hexose sugars to their corresponding lactones and aldobionic acids (see Rand, Qvist, Walter, & Poulsen, 2006 and references therein).

The integration of information available for *C. crispus*, in particular genome annotation, will be used to reconstruct metabolic networks; however, more metabolic profiling is certainly needed to complete existing observations.

3.10 CELL WALL BIOLOGY

Red algal cell walls are a composite material often made of cellulose microfibrils embedded in a matrix composed of polysaccharides, and to a lesser extent, proteins and aromatic substances. In *C. crispus* the matrix components are highly sulphated galactans known as carrageenans. They are made up of linear chains of disaccharidic motifs of D-galactose residues with alternating α(1–3) and β(1–4) linkages and classified according to the number and position of sulphate esters and by the occurrence of a 3,6-anhydro bridge in the α-linked residue. The κ-, ι- and λ-carrageenans are respectively substituted by one, two or three sulphate ester groups per digalactose repeating unit (Figure 3.4). *Chondrus crispus* synthesis all three of these carrageenans although variations are observed depending on the life stage. Carrageenans in gametophytes are a mixture of κ- and ι−carrageenans (~70 and ~20%), with the presence of low amount of biosynthetic precursor motifs (~8% μ-carrageenan and 2% ν-carrageenan). The tetrasporophyte synthesise only λ-carrageenans (Chopin, Bodeau-Bellion, Floc'h, Guittet, & Lallemand, 1987; Tasende, Cid, & Fraga, 2012). Carrageenans naturally occur as heteropolymers composed of a sequence of several moieties, and the use of dedicated enzymes from marine bacteria has lately served to address the specific distribution patterns of the carrabiose units within the chains (Guibet et al., 2008; Jouanneau, Boulenguer, Mazoyer, & Helbert, 2010).

As for land plants, the amorphous matrix polysaccharides are expected to be interconnected to other polysaccharides or crystalline polysaccharides and thus contribute to mechanical resistance, cell expansion, and cell wall cohesion (Carpita & McCann, 2000). However, very little is known of the nature of these polysaccharides in red algae. They represent a small portion of the wall (1–8% of the dry weight). Cellulose fibrils are the most commonly found polymer, but additional polymers, such as crystalline β(1–4)-D-mannans, β(1–4) or β(1–3)-D-xylans, as sulphated α(1–3)-D-mannans or sulphated β(1–3/1–4)-D-glucans, have also been reported in various red algal species (Popper et al., 2011). Their existence in *C. crispus* still needs to be established.

The current knowledge on cell wall metabolism in red seaweed is very limited. The genome sequence of *C. crispus* allows some predictions on the cell wall metabolic pathways (Collén et al., 2013). The carrageenan

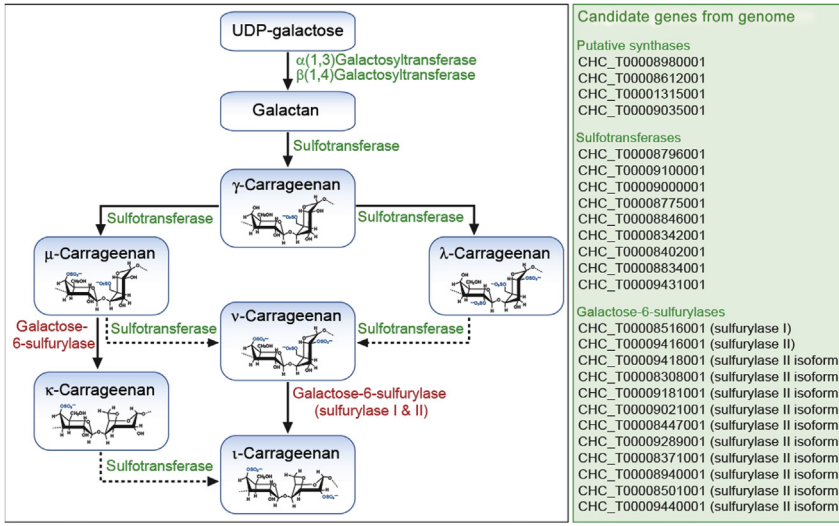

Figure 3.4 Putative carrageenan biosynthesis pathway in *Chondrus crispus* with the corresponding candidate genes retrieved from the genome sequence. Only the conversions of μ- to κ-, and ν- to ι-carrageenan, were enzymatically demonstrated in *C. crispus*.

biosynthesis pathway is yet not fully understood and most of the steps stay therefore highly speculative. It was proposed that carrageenans are first synthesised in the Golgi apparatus as a linear and neutral backbone of galactan by galactosyl transferases that catalyse the polymerisation of galactose residues (Figure 3.4). The alternation of α(1–3) and β(1–4) linkages would suggest the activity of two types of glycosyltransferases. Four genes homologous to chondroitin synthases were identified in *C. crispus*. These enzymes are involved in the biosynthesis of the sulphated glycosaminoglycans in animals and therefore the red algal homologue is a good candidate for the biosynthesis of carrageenans. Following polymerisation, the initial sulphation is likely to occur in the Golgi apparatus by sulphotransferases. In *C. crispus*, nine genes similar to carbohydrate sulphotransferases were identified. Their animal homologues are involved in the biosynthesis of glycosaminoglycans, suggesting again that genes are likely involved in the carrageenan sulphation. The sulphated galactan obtained is thereafter transported into the wall where galactose-6-sulphurylases remove the C6-sulphate from precursors to form the 3,6-anhydro bridges. This final step of carrageenan synthesis was demonstrated in *C. crispus* gametophytes with the characterisation of two distinct galactose-6-sulphurylases, named

sulphurylase I and II, which convert ν- into ι-carrageenan (Genicot-Joncour et al., 2009). An enzymatic activity catalysing the conversion of μ- to κ-carrageenan has also been demonstrated in both life cycle phases of *C. crispus* (Wong & Craigie, 1978), but the corresponding gene is unknown. The *C. crispus* genomic analysis retrieved two genes identical to the previously cloned genes of sulphurylases I and II, but also ten additional paralogous genes of sulphurylase II (Figure 3.4). Among the nine sulphotransferases identified in the *C. crispus* genome, some of them might also be present into the wall for further modifications of the carrageenan chains. Finally, while sulphatases were supposed to be involved in the carrageenan remodelling of the growing wall, no homologue has been identified in the *C. crispus* genome. This result suggests that no modification in its sulphation pattern occur in carrageenan after its biosynthesis, or that new families of sulphatases may exist in the genome. By contrast, three glycosyl hydrolases related to κ-carrageenases from marine bacteria (Michel, Chantalat, Duee, et al., 2001; Michel, Chantalat, Fanchon, et al., 2001) were identified in the genome sequence and are likely involved in cell wall remodelling.

Like in land plants, the cellulose microfibrils in red algae are synthesised by clusters of cellulose synthases (CESAs) in terminal complexes (TCs), which move in the plasma membrane. However, the morphologies of the TCs and the cellulose microfibrils they produce differ from those of land plants: the TCs are organised in linear rows, randomly distributed in the plasma membrane and the resulting microfibrils show a flat-ribbon or a rectangular-parallelepiped morphology (Tsekos, 1999; Tsekos, Reiss, & Schnepf, 1993). At least three different CESA proteins are required to form a functional rosette TC in plants (Mutwil, Debolt, & Persson, 2008), while the minimum number of recruited CESAs in functional TCs in red algae is unknown. In *C. crispus*, the genome sequence analysis retrieved two CESA genes, similar to those already described in the red algae *Porphyra* sp. and *Griffithsia monilis*. However these red algal CESAs have a distinct origin to those found in land plants and their acquisition probably predated the primary endosymbiosis event. A third CESA gene is found in *C. crispus*, unrelated to the previous, and probably of an ancestral bacterium origin. Such differences within the Archaeplastida lineage might explain the structural variation in the TC organisation and the cellulose microfibrils in red algae compared to land plants. Finally, *Chondrus* also possesses GH5, GH6 and GH45 cellulases, which are absent in plants and that might be involved in remodeling of the cellulose fibrils.

Land plants require a rigid structure to support them against the pull of gravity, making crystalline cellulose an important part of the wall. By contrast marine algae need more flexible structures to accommodate the varying stresses of tidal and wave action and a cell wall mostly composed of carrageenans might fulfill this role. However the physiological significance of the variations in carrageenan composition in relation to mechanical, hydration or electrochemical regulations is still matter of debate (Kloareg & Quatrano, 1988). The *Chondrus* gametophyte, with strong gelling κ-type carrageenans, has been shown to be mechanically superior to the tetrasporophyte, with nongelling λ-type carrageenans (Carrington, Grace, & Chopin, 2001), however, this is of no impact on the distribution of the life history phases in natural populations of *C. crispus* (Garbary, Tompkins, White, Corey, & Kim, 2011). Regarding the hydration properties, if one assumes that sulphated carrageenans protect against desiccation by enhancing water absorption, we would expect the littoral populations of *C. crispus* to have increased carrageenan contents compare to the sublittoral ones. Again such assumption has yet failed to be clearly established (Fuller & Mathieson, 1972).

3.11 COMMERCIAL USES

The majority of fresh seaweeds, are not very palatable due to their texture, so they must be processed in some manner to improve their mouthfeel. In the eighteenth century, the most common method of household processing involved cooking in some way, thus *C. crispus* was recognised very early for its special thickening characteristics. Other rhodophytes, such as *Palmaria* and *Porphyra*, became the seaweeds of choice for direct consumption and as nutritional ingredients in foods, while *C. crispus* became valuable in the food and pharmaceutical industries. Less attention, therefore, was given to its potential health and nutritional benefits as a natural food.

The Irish moss based carrageenan industry in North America also developed rapidly in the early 1940s due to the pioneering work of Jacques Wolf and Company, Krim-Ko and Kraft Foods (Lewis, Stanley, & Guist, 1988). The Krim-Ko operation at Scituate, Massachusetts, changed hands to become Seaplant Corporation, while the Kraft Food operation of South Portland, Maine, was taken over by Stauffer Chemical Company in 1970 and was later closed. The Algin Corporation of America, Rockland, Maine, also began processing Irish moss soon after WWII to become a major carrageenan producer by the mid-1950s. In addition, it licensed carrageenan processing technology to SATIA of France (Lewis et al., 1988). Marine

Colloids Inc., of Rockland, Maine, was formed by an amalgamation in 1959 of the Algin and Seaplant Corporations, and by 1977 it, in turn, became a Division of FMC Corporation to remain as the sole manufacturer of carrageenan in the USA.

Commercial applications for Irish moss extract depend upon a detailed knowledge of the chemical and physicochemical properties of these phycocolloids. In brief, key events included the resolution of hot water extracts from *C. crispus* into soluble and gelling fractions based upon their sensitivity to potassium ions (Smith & Cook, 1953). The authors coined the terms 'λ-carrageenin' and 'κ-carrageenin' for these respective fractions. The proportion of the κ-/λ- carrageenan fractions controls the performance of a given extract in milk reactivity and other valued functions of the phycocolloids (Witt, 1985; Stanley, 1987). This ratio issue was resolved when it was established that the sporophyte generation of *C. crispus* produced only λ-carrageenan devoid of 3,6-anhydrogalactose, while the κ-family of carrageenans characterised both the gametophyte phases of the alga (McCandless, Craigie, & Walter, 1973). The thorough historical review by Stortz (2005) discusses the pioneering studies by Rees (1972) and his colleagues.

In the early 1970s *C. crispus* from Canada provided 75% of the world's production of carrageenan but, by 1992, *C. crispus* represented only 3.8% of the global harvest of carrageenophytes with Canada providing a mere 12% (Chopin, 1998; Pringle & Mathieson, 1987). By the late 1990s, *C. crispus* from Brittany, Vendée and Normandy represented only 9% of the carrageenophytes supplying the French carrageenan industry (Kaas, 1998). In Ireland the bulk of the *C. crispus* harvest is sold locally where it is used primarily in cooking and as a natural cold remedy (Guiry & Hession, 1998).

Acadian Seaplants Limited, in conjunction with the National Research Council of Canada and other government partners, developed a unique and innovative food product from cultivated *C. crispus*. It is utilised in a rehydrated form primarily in the *kaiso* salad market of Japan, with some usage directed to soups and garnishes due to its unique colours, shape and consistent quality. However, the global dietary seaweed market is currently dominated by cultivated species such as *Saccharina japonica* (kombu), *Undaria pinnatifida* (wakame) and *Pyropia* (*Porphyra*) spp. (Ohno & Largo, 1998).

Research shows there are many therapeutic characteristics associated with seaweeds in general and a number of species from the dominant three genera have been investigated. *Chondrus crispus* possesses characteristics typical of most seaweeds, such as antioxidant capacities and mineral content (Cornish & Garbary, 2010; Ruperez, 2002; Sangha et al., 2013), but it also

provides specialised fibre in the form of both soluble and insoluble or fermentable components (Rupérez & Toledano, 2003). These are important in gut health as fibre type has been demonstrated to affect subjective appetite, acute energy intake, long-term energy intake and body weight, due in large part as a function of the various physicochemical properties of the dietary fibres (Wanders et al., 2011). Other research studies specific to *C. crispus* have demonstrated potential for therapeutic benefits in terms of anticoagulant activity (Lee, Athukorala, Lee, & Jeon, 2008), lipid induced nitric oxide inhibition (Banskota et al., 2013) and enhanced immune response (Liu, Hafting, Critchley, Banskota, & Prithiviraj, 2013).

Irish moss extracts provide valuable ingredients for cosmetic applications, in part as a result of their special hydrocolloid properties (Witt, 1985) and they also possess components with sunscreen and antiageing potential (Franklin, Kräbs, & Kuhlenkamp, 2001; Kräbs, Bischof, Hanelt, Karsten, & Wiencke, 2002; Kräbs et al., 2004; Sinha, Singh, & Häder, 2007). Tank culture permits close control of crop traceability and management. The optimisation of production rates is possible and opportunities for the appearance and isolation of phenotypic mutants are enhanced (van der Meer, 1981). Some of these may possess unique characteristics of commercial value and colour mutations enriched in blue pigment is an example (Cornish, O'Leary, & Garbary, 2013).

The long-term utilisation of Irish moss as a food and its well studied physiology make *C. crispus* a useful and versatile commercial product. Tank culture provides opportunities to exploit this alga as a vehicle for enhanced nutrition or increased functionality. Maximising control over the culture environment for *C. crispus* presents possibilities for the enhancement of useful secondary metabolite compounds and antioxidant capacity by upregulating its stress genes (Collén et al., 2007; Collén et al., 2006a; Yakovleva & Titlyanov, 2001). Cultivated *C. crispus* is now well positioned to become a global commercial success, again.

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