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Genomics of brown algae: current advances and future prospects

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Abstract

The analysis of the complete genome sequence of the filamentous brown alga *Ectocarpus* provided many new insights into brown algal biology and has improved our understanding of how this organism has adapted to its seashore environment. Since the publication of the genome sequence in 2010, numerous studies have continued the analysis of the constituent genes or have combined genome data with experimental work, allowing progress in several key areas, including metabolism and reproductive biology. *Ectocarpus* will continue to be exploited as a model organism in future years, but genomic approaches should also be extended to additional brown algal species in order to fully exploit the diversity of this phylogenetic group and to facilitate the application of new knowledge to economically important seaweeds such as kelps.

Keywords brown algae; *Ectocarpus siliculosus*; genome sequence; biotechnology

Brown algae

Brown algae are major constituents of many rocky shore ecosystems around the planet, particularly in the colder regions of the oceans. These organisms, which are all multicellular,

belong to the stramenopile clade, along with diatoms and oomycetes, and are therefore very distantly related to both animals and terrestrial plants.

The *Ectocarpus* genome sequence

The recently published genome sequence of the filamentous brown alga *Ectocarpus* (Cock et al., 2010) has provided many new insights into the biology and evolutionary history of the brown algae. Several gene families were identified that potentially play an important role in adapting *Ectocarpus* to the harsh conditions of its shoreline habitat, where it is subjected to a broad range of both abiotic and biotic stresses. For example, the genome contains a large number of light harvesting complex (LHC) genes, including a cluster of genes that belong to the L1818 family of light-stress related LHCs. This expanded gene family and other photosynthetic genes such as a light-independent protochlorophyllide reductase (DPOR) are thought to enable *Ectocarpus* to adapt to the highly variable light conditions of the intertidal and upper subtidal zones. Other metabolic components such as flavonoid pathway enzymes and a diverse complement of enzymes involved in the metabolism of reactive oxygen species may be involved in protection against abiotic stresses such as ultraviolet radiation.

The cell walls of brown algae exhibit several unique features (Kloareg and Quatrano, 1988). Cellulose is present, as in land plants, but this polysaccharide is a relatively minor component and alginates and fucoidans (anionic polysaccharides) constitute the major constituents. Alginates provide the cell wall with both strength and flexibility, and thereby contribute to adapting brown algae to the coastal environment. Phylogenetic analysis of the genes implicated in cell wall biosynthesis in *Ectocarpus* suggested that its cellulose synthesis pathway was inherited from a red alga (Michel et al., 2010a) via the secondary endosymbiosis event that provided the brown algae with a plastid (Reyes-Prieto et al., 2007). In contrast, the terminal steps of the alginate biosynthesis pathway appear to have been acquired via a horizontal

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gene transfer event involving an actinobacterium (Michel et al., 2010a).

The pathways that synthesise carbon storage molecules in *Ectocarpus* also appear to have a complex evolutionary history. Brown algae store carbon principally in the form of mannitol and the β -1,3-glucan laminarin (Percival and Ross, 1951). The mannitol biosynthetic pathway appears to have been acquired via a horizontal gene transfer from an actinobacterium (perhaps at the same time as the terminal steps of the alginate pathway?), whereas a β -1,3-glucan biosynthetic pathway was probably already present in the ancestor of the stramenopiles (Michel et al., 2010b).

The brown algae are one of only a small number of eukaryotic groups that are considered to have evolved complex multicellularity and analysis of the genome sequence identified several features that may have been important for the emergence of multicellularity in this group (Cock et al., 2010). These included the retention, during evolution, of diverse families of ion channels, transcription factors, GTPases and Rad51 family proteins. One particularly interesting feature was the presence of a family of membrane-spanning receptor kinases, which appears to have been acquired by the brown algal lineage since they diverged from the diatoms. Receptor kinase families evolved independently in both the animal and the green plant lineages and, in both cases, the emergence of these families have been linked to the transition to multicellularity. The independent emergence of similar molecules in the brown algae strongly supports this hypothesis.

The acquisition of a flexible cell wall containing polysaccharides such as alginates and fucoidans may also have played an important role during the transition to multicellularity, allowing the formation of large, complex bodyplans that were capable of resisting the disrupting effects of wave action.

The *Ectocarpus* genome exhibits several unusual structural features that have not been found in genomes from other stramenopile groups, such as the diatoms and the oomycetes. *Ectocarpus* genes tend to be rich in introns (seven per gene on average) and these introns, like the 3' untranslated regions, are relatively long (average intron and 3'UTR length is 704 and 848 bp, respectively). Moreover, genes are often clustered closely together on the chromosome, and one consequence of this is that intron sequence makes up an exceptionally large proportion of the *Ectocarpus* genome (40%). The arrangement of genes along the chromosome is also surprisingly ordered in *Ectocarpus* in the sense that 61.5 % of genes are followed by a gene located on the opposite strand of the DNA, resulting in genes alternating between strands as one scans along the chromosome. It is not known whether this alternating arrangement of genes is of functional importance; adjacent genes tended to show similar patterns of expression in response to different stresses, but there was no evidence that this bias was related to the orientation of the

genes (Cock et al., 2010).

Exploiting the *Ectocarpus* genome sequence to investigate brown algal biology

Since its publication in 2010, the *Ectocarpus* genome sequence has been exploited in several different ways. Bioinformatic analysis of the genome sequence has continued, providing insights both into specific aspects of brown algal biology and into events on a broader scale across the eukaryotic tree. For example, recently a detailed analysis of the predicted components of the mitochondrial protein import apparatus, together with associated protease activities, indicated that many of the components of this system are very ancient and were probably present in the common ancestor of all the major extant eukaryotic groups (Delage et al., 2011). Other components of the system appear to have undergone replacement or rearrangement events, or to have emerged as new components during evolution. This is the case for outer membrane receptors for example. A similar study, which focused on chlorophyll-binding proteins, favoured a hypothesis in which the LI818 family of chlorophyll-binding proteins, which are broadly implicated in stress responses, originated in a chlorophyll a/c-containing organism and was then transferred horizontally to the green lineage (Dittami et al., 2010).

In other studies, bioinformatic analysis of the genome sequence has been combined with complementary experimental approaches. For example, it has long been known that both male and female gametes of *Ectocarpus* can germinate parthenogenetically and that the partheno-sporophytes that result are able to produce meio-spores (the initial cell of the gametophyte generation) in unilocular sporangia (Müller, 1967). How they are able to do this has been a mystery because meio-spores are normally derived from a meiotic cell division that is followed by several mitotic divisions, and it has been difficult to see how this could occur when the initial cells of the partheno-sporophytes are haploid gametes. However, careful analysis of ploidy levels in the cells of developing partheno-sporophytes indicated that about one third of these individuals underwent an endoreduplication event very early in development (Bothwell et al., 2010a; Bothwell et al., 2010b). These diploid individuals can then initiate meiotic cell division in the same manner as diploid sporophytes derived from the fusion of two gametes. A complementary bioinformatic analysis of the genome sequence identified a number of genes that potentially play a role in mediating the endoreduplicative cell division (Bothwell et al., 2010b). These results therefore explained how one third of the partheno-sporophytes produce meio-spores, but what about the remaining two thirds? It appears that these individuals employ non-reductive apomeiotic cell divisions to produce their meio-spores, allowing the production of haploid

zoids from a haploid mother cell (Bothwell et al., 2010b).

Another recent study proposed that auxin plays a role in the regulation of morphogenesis in *Ectocarpus* and this hypothesis was supported by the identification of potential components of auxin biosynthetic pathways (Le Bail et al., 2010).

As mentioned above, brown algae have an unusual carbon storage system involving the production of mannitol and the β -1,3-glucan laminarin. Analysis of the genome sequence has identified several potential components of the biosynthetic pathways for these two compounds and a recent study confirmed the predicted biochemical activity of the first enzyme in the mannitol biosynthesis pathway, mannitol-1-phosphate dehydrogenase (Rousvoal et al., 2011). A similar biochemical characterisation has been carried out for the *Ectocarpus* GDP-mannose dehydrogenase, which produces the alginate precursor GDP-mannuronic acid (Tenhaken et al., 2011). These two studies represent the first steps towards experimental analysis of gene function in *Ectocarpus*.

An expression microarray has been developed based on the cDNA sequence data generated during the *Ectocarpus* genome project (Dittami et al., 2009). This microarray has been used to characterise modifications to the transcriptome in response to a variety of different external stimuli and developmental modifications. For example, the transcriptome of *Ectocarpus* sporophytes was shown to undergo extensive modifications in response to a variety of different stresses (hyposaline, hypersaline and oxidative stress), even when the stress was mild (Dittami et al., 2009). The EST-based microarray has also been used to track changes in transcript abundances during the transition between the sporophyte and gametophyte generations of the life cycle (Coelho et al., 2011). This analysis identified trends in changes in gene expression that may have been correlated with the functional roles of each generation of the life cycle. Two genetic loci have been identified that play an important role in regulating the alternation between the sporophyte and gametophyte generations of the life cycle (Coelho et al., 2011; Peters et al., 2008) and the EST-based microarray has been used to assay transcript abundances in strains carrying either one of these mutations or a combination of both mutations. Comparisons with the transcriptomes of the wild type sporophyte and gametophyte generations have allowed the identification of potential effector genes that act downstream of these key regulators (Coelho et al., 2011). A similar analysis has been carried out for the *etoile* mutant, which exhibits a modified pattern of morphological development (Le Bail et al., 2011). Information from the genome sequence, together with additional genetic tools such as a microsatellite-based genetic map (Heesch et al., 2010), is currently being exploited to identify the genes corresponding to the life cycle and morphological mutants described above by positional cloning.

Where next for brown alga genomics?

Future work on *Ectocarpus* is expected to provide further insights into diverse aspects of brown algal biology but there are also several strong arguments for applying genomic approaches, particularly genome and/or transcriptome sequencing, to other members of the brown algae. As a group, brown seaweeds exhibit a broad range of characteristics in terms of their morphology, biochemistry and reproductive biology. For example, mating systems range from isogamous (in which the male and female gametes are identical or nearly identical) to oogamous systems, with large, non-motile egg cells and small, motile male gametes. Brown algae also exhibit a broad range of different life cycles including haploid-diploid life cycles with both sporophyte and gametophyte generations, and diploid life cycles with only one multicellular stage. Moreover, the relative sizes of the sporophyte and gametophyte generations of haploid-diploid life cycles can be highly variable across taxonomic groups. Phylogenetic analysis has indicated that reproductive characteristics such as mating type and life cycle structure are relatively plastic on an evolutionary timescale, switching between different systems having occurred multiple times during the emergence of the brown algae as a group (Silberfeld et al., 2010).

There are several other areas where it would be of interest to extend genomics approaches to additional brown algae. For example, the *Ectocarpus* genome has provided some clues as to how multicellularity may have evolved in the brown algae, but *Ectocarpus* itself does not exhibit a high degree of morphological complexity and it would be interesting to look at the genome composition of more developmentally complex brown algae such as kelps. Biochemical characteristics can also vary considerably across the brown algae. For example halide metabolism would appear to be considerably less developed in *Ectocarpus* than in kelps such as *Laminaria digitata* (Cock et al., 2010; Colin et al., 2003). Taken together, these differences between brown algal species across a broad range of characteristics provide a strong argument for more extensive exploration of brown algal genomes and transcriptomes. Moreover, a deeper understanding of the brown algae would not only be of interest from a fundamental point of view but would also open up new possibilities for the industrial exploitation of this group of organisms. One consequence of the very different phylogenetic history of the brown algae, compared to most well studied organisms, is that they have evolved novel metabolic processes, making them interesting targets for the discovery of novel biomolecules with industrial applications (Klarzynski et al., 2003; Mc Hugh, 2003). Note that the brown algae are also attracting growing interest as a potential source of biomass for biofuel production, both because of their high productivity and because they would not compete with terrestrial crops for arable land (Bartsch et al., 2008). Brown algae are also the most important organisms in most coastal

ecosystems, in terms of biomass, where they can form submerged forests that rival terrestrial forests in size. These marine forests perform important ecosystem services in terms of carbon fixation and the creation of niches for a broad range of other marine organisms.

Given that there are strong arguments for extending genome and transcriptome analysis to additional brown algae, which species should be targeted? Kelps exhibit considerable developmental complexity and a high potential for biotechnological exploitation, and it would clearly be of interest to obtain genomic sequence information for a member of this group. There are several interesting candidates amongst commercially exploited kelps, including *Undaria*, *Laminaria*, *Saccharina* and *Macrocystis* species. Of these, *Macrocystis* is particularly interesting because of its capacity to produce biomass. This brown alga is one of the biggest organisms on the planet, growing up to lengths of 60 metres and is also one of the fastest growing, extending by up to 50 cm per day. *Macrocystis* is already exploited on a large scale for alginate production and there is currently considerable interest in growing this alga as a source of biomass for biofuel production. On the other hand, species of *Undaria* and *Saccharina* are widely maricultured in north-east Asia and therefore also represent interesting candidates.

The Ectocarpales would also be an interesting group for additional genome sequencing both because of their relatedness to the sequenced species (*Ectocarpus siliculosus* is a member of this order) and because they exhibit a large degree of diversity for several different features, particularly in terms of their reproductive biology. Moreover, these algae have relatively small genomes compared to most brown algae (around 200 Mbp) making them more accessible to genome sequencing.

One key area for future brown algal research will be host-parasite and host-pathogen interactions. Maricultured kelps, like any crop species, are prone to attacks by pathogens, which may be bacteria and unicellular or multicellular eukaryotes (Gachon et al., 2010). *Ectocarpus* is not only susceptible to pathogens but may also attack large algae on which it lives either as an epiphyte or as an endophyte (Russell, 1983a; Russell, 1983b). Transcriptomic and genome studies of such model host-pathogen systems are expected to provide general insights into both attack and defence mechanisms (Grenville-Briggs et al., 2011).

Based on the above arguments, we expect a rapid expansion of brown algal genomics in the coming years, which will make significant contributions both to our understanding of fundamental biological processes and to biotechnology.

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