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Genetic regulation of life cycle transitions in the brown alga *Ectocarpus*

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The life cycle of an organism is one of its most elemental features, underpinning a broad range of phenomena including developmental processes, reproductive fitness, mode of dispersal and adaptation to the local environment. Life cycle modification may have played an important role during the evolution of several eukaryotic groups, including the terrestrial plants. Brown algae are potentially interesting models to study life cycle evolution because this group exhibits a broad range of different life cycles. Currently, life cycle studies are focused on the emerging brown algal model *Ectocarpus*. Two life cycle mutants have been described in this species, both of which cause the sporophyte generation to exhibit gametophyte characteristics. The *ouroboros* mutation is particularly interesting because it induces complete conversion of the sporophyte generation into a functional, gamete-producing gametophyte, a class of mutation that has not been described so far in other systems. Analysis of *Ectocarpus* life cycle mutants is providing insights into several life-cycle-related processes including parthenogenesis, symmetric/asymmetric initial cell divisions and sex determination.

Multicellular organisms from diverse groups across the eukaryotic tree exhibit a variety of life cycles, differing essentially in the relative importance of the diploid and haploid phase¹. For most animal species the diploid phase of the life cycle is the only multicellular stage, whereas flowering plants exhibit an alternation between two multicellular generations, the macroscopic, diploid sporophyte and the microscopic, haploid gametophyte. Modifications to life cycle structures may have played an important adaptive role during the evolution of some major eukaryotic groups. In the green lineage, for example, there appears to have been a gradual tendency towards increasing dominance of the diploid generation as plants adapted to the terrestrial environment. As a result, the gametophyte generation in angiosperms (i.e. the pollen grain or the embryo sac) has been reduced to a structure consisting of just a few cells.

Despite the importance of life cycles, from both an evolutionary and a developmental perspective, little is known about how life cycle transitions are regulated at the molecular level. Brown algae are a particularly interesting group for the study of life cycle regulation and evolution because they exhibit a broad range of different cycles, ranging from isomorphic, haploid-diploid (with two morphologically identical generations) to diploid (with only one multicellular generation). In addition, brown algal life cycles are often quite complex, sometimes including several variant pathways. The filamentous brown alga *Ectocarpus* has a haploid-diploid life cycle that involves alternation between two morphologically similar generations but a number of variations on this basic cycle are possible. For example, gametes that fail to fuse with a gamete of the opposite sex can germinate parthenogenetically to produce haploid partheno-sporophytes^{2,3}. Such variant life cycles provide valuable information about the influence of factors such as ploidy and meiosis/fertilisation on life cycle transitions.

Another, more direct, approach to elucidate the mechanisms that control life cycle progression is to screen for mutant individuals in which these processes are modified. This type of screen has been carried out with *Ectocarpus* and two life cycle mutants have been described so far. The first mutation, *immediate upright* (*imm*), causes partial conversion of the sporophyte generation into a gametophyte⁴. The *imm* sporophyte exhibits several morphological features typical of the gametophyte, but nonetheless produces spores and not gametes. The more recently described *ouroboros* (*oro*) mutation causes conversion of the the sporophyte into a full-functional, gamete-producing gametophyte⁵. In crosses, *imm* and *oro* behaved as two independent, single locus, recessive Mendelian factors⁵. Microarray analyses of changes in mRNA abundances in the *imm* and *oro* mutants compared to wild type samples suggested that both loci act as master regulators, influencing the expression of a large number of downstream genes. This is a typical characteristic of homeotic genes and, in this respect, it is interesting to note that *oro* can be considered to belong to a novel class of homeotic gene, causing homeotic conversion at the level of the entire bodyplan rather than effecting just one organ or tissue.

Characterisation of the *imm* and *oro* mutations is expected to provide insights into several aspects of life cycle regulation. For example, gametes from *Ectocarpus* strains carrying the *oro* mutation germinate parthenogenetically to give partheno-gametophytes rather than partheno-sporophytes. As the former is the wild type situation in several other species of brown algae, such as *Myriotrichia clavaeformis* for example⁶, it will be interesting to determine whether variability with respect to this character in different brown algal species is linked to variability at the *ORO* locus.

Life cycle mutants have also been used to investigate the relationship between early development and life cycle progression. The two generations of the *Ectocarpus* life cycle exhibit radically different patterns of

early development⁴. The initial cell of the gametophyte (a meio-spore) undergoes an *asymmetric* division to produce a rhizoid and an upright filament, whereas the sporophyte initial cell (a zygote) divides *symmetrically* to produce a basal filament that is strongly attached to the substratum, upright filaments and rhizoids only being produced later in development. The phenotype of the *imm* mutant demonstrates that the pattern of initial cell division can be uncoupled from life cycle generation determination because functional sporophytes develop from an asymmetric initial cell division in this mutant.

The sex of *Ectocarpus* gametophytes is determined genetically by a single Mendelian locus. The *oro* mutation is not linked to the sex locus, so it was possible to produce both male and female strains carrying this mutation. Crosses between *oro* males and *oro* females resulted in diploid individuals that developed as gametophytes and produced diploid gametes⁵. The diploid gametophytes produced by this cross provided additional evidence that the life cycle generation is not strictly determined by ploidy in *Ectocarpus* (as was already suggested by several observations, including the generation of haploid partheno-sporophytes from parthenogenic gamete germination, mentioned above). Sex determination in *Ectocarpus* is unusual in that sexuality is expressed during the haploid gametophyte generation as a result of the male and female haplotypes of the sex locus operating independently in male and female individuals. Interestingly, the *oro* homozygous, diploid gametophytes produced by the above cross were males, indicating that the male haplotype of the sex locus is dominant over the female haplotype when they occur in the same sexual individual⁵.

Global analysis of gene expression in wild type strains and life cycle mutants allowed the identification of a large collection of genes whose transcripts accumulated to significantly different levels on the sporophyte and the gametophyte⁵. Analysis of the predicted functions of these genes indicated a tendency for genes associated with primary metabolism (including carbohydrate and lipid metabolism) and related functions such as transport to be over-represented amongst the transcripts that accumulated to higher levels in the sporophyte, whereas genes associated with protein synthesis and modification and other basic cellular processes, such as cell cycle and DNA replication, were over-represented amongst the transcripts that accumulated to higher levels in the gametophyte, suggesting that there may be marked physiological differences between the two generations of the life cycle. This observation is consistent with one of the ideas that has been put forward to explain the stability of haploid-diploid life cycles over long timescales - that the two generations of the life cycle may be adapted to different ecological niches, allowing survival in a changing environment^{1,7}. There is some evidence that the two generations of *E. crouaniorum* may be adapted to different environmental conditions⁸. The small sporophyte of this species, which grows on stones or shells, is present all year round, whereas the larger gametophyte is found only in the spring, suggesting that the sporophyte generation might be adapted to more extreme physical conditions whereas the role of the gametophyte would be to grow rapidly under favourable growth conditions. More information about the niches of individual generations of different *Ectocarpus* species in the wild is necessary to further investigate the ecological role of each life cycle generation in these organisms.

From a developmental point of view, the phenotypes of the *imm* and *oro* mutants could be due either to failure to initiate the sporophyte pathway or failure to repress the gametophyte pathway. Microarray analysis provided evidence that the transition from the sporophyte to the gametophyte generation involved predominantly gene repression⁵, suggesting that the principal function of the *imm* and *oro* genes may be to repress the gametophyte developmental pathway. If this is the case, then the sporophyte

developmental program could be considered to be the default pathway. This may have implications for evolutionary modifications of life cycles in the brown algae.

Current work aimed at identifying the genes affected by the *imm* and *oro* mutations by positional cloning should not only begin to elucidate the molecular mechanisms that regulate life cycle progression in *Ectocarpus* but should also shed light on other fundamentally important processes such as early development and parthenogenesis. Importantly, a growing number of genetic and genomic tools are being made available for *Ectocarpus*⁹⁻¹³, including the complete genome sequence¹⁴. The availability of these tools will increasingly facilitate the use of this emerging model organism to study many aspects of brown algal biology¹⁵ including life cycle regulation.

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