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# Alternation of Generations in Plants and Algae

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## Abstract

Photosynthetic organisms are found in most of the branches of the eukaryotic tree of life, and these organisms have diverse life cycles. There has been a tendency toward dominance of the diploid phase of the life cycle in the land plant lineage, and recent analyses suggest a similar trend in the brown algae. A number of hypotheses have been proposed to explain the evolutionary stability of different types of life cycle, and in some cases these hypotheses are supported by empirical studies. Molecular analyses are elucidating the regulatory molecules that control life cycle progression and are providing insights into the developmental pathways associated with the construction of each generation of the life cycle.

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## Keywords

Diploid • Epigenetic • Gametophyte • Haploid • Sporophyte

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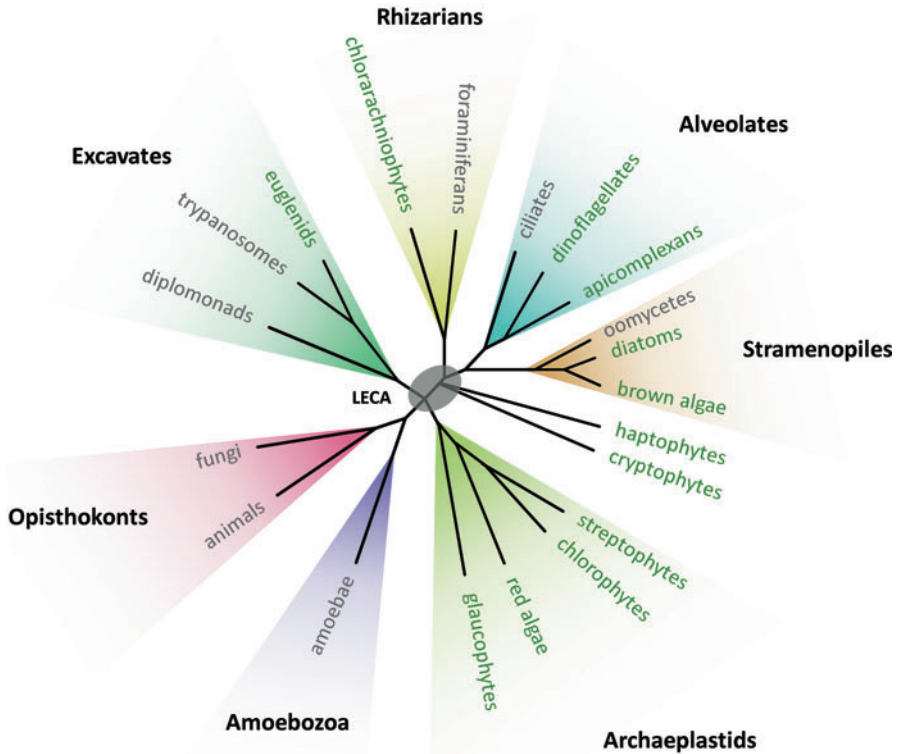
## Introduction

The term “algae” groups together photosynthetic organisms from a broad range of lineages, with representatives in almost all the supergroups of the eukaryotic tree of life (Fig. 1, see the glossary for definitions of the terms used). From a strict, taxonomic point of view, “plants” correspond to the kingdom Plantae (equivalent to the modern group Archaeplastida; Fig. 1), but this term is often used loosely to include any macroscopic photosynthetic organism, particularly those in terrestrial habitats. In any event, plants are therefore a subset of the algae.

While it is preferable to use more taxonomically precise names when discussing phylogeny, the terms plants and algae are nonetheless extremely useful because they group together organisms that share many common biological features that stem from their autotrophic lifestyles based on photosynthesis. The broad taxonomic distribution of these organisms can be traced back to the various mechanisms whereby they have acquired the ability to carry out photosynthesis. For algae in the archaeplastid group (which includes green algae, red algae and glaucophytes; Fig. 1), photosynthetic capacity arose due to a primary endosymbiotic event, which involved the engulfment of a cyanobacterium by a common ancestral eukaryotic cell. The enslaved cyanobacterium became the plastid.

The other eukaryotic lineages acquired photosynthesis by more complex secondary (and perhaps even tertiary) endosymbiotic events, in which a photosynthetic eukaryote (usually a red or green alga) was enslaved by another eukaryotic cell. It is this process of secondary endosymbiosis that has led to the occurrence of photosynthetic organisms in such a diverse array of eukaryotic supergroups (stramenopiles, alveolates, rhizarians, haptophytes, cryptophytes, and excavates). Given the complicated evolutionary history of plants and algae, it is not surprising that they exhibit a high level of diversity with regard to many characters, including their life cycles, the feature that will be discussed in this chapter.

The basic eukaryote sexual life cycle involves an alternation between two key processes: meiosis, which allows the chromosome number to be reduced by half, and syngamy or gamete fusion, which restores the level of ploidy by bringing together the chromosomes of the fusing gametes in a single nucleus within the zygote (John 1994). Before meiosis the cells are diploid, after meiosis they are haploid, and syngamy restores the diploid state. Variations on this basic life cycle can be defined based on the relative importance of these two phases, i.e., whether the organism grows (undergoes mitotic cell divisions) during the haploid or the diploid phase, or both (Fig. 2). When growth occurs during the diploid phase, the life cycle is called a diploid life cycle (the human life cycle is one example). When growth occurs during the haploid phase, the life cycle is called a haploid life cycle (e.g., that of the green

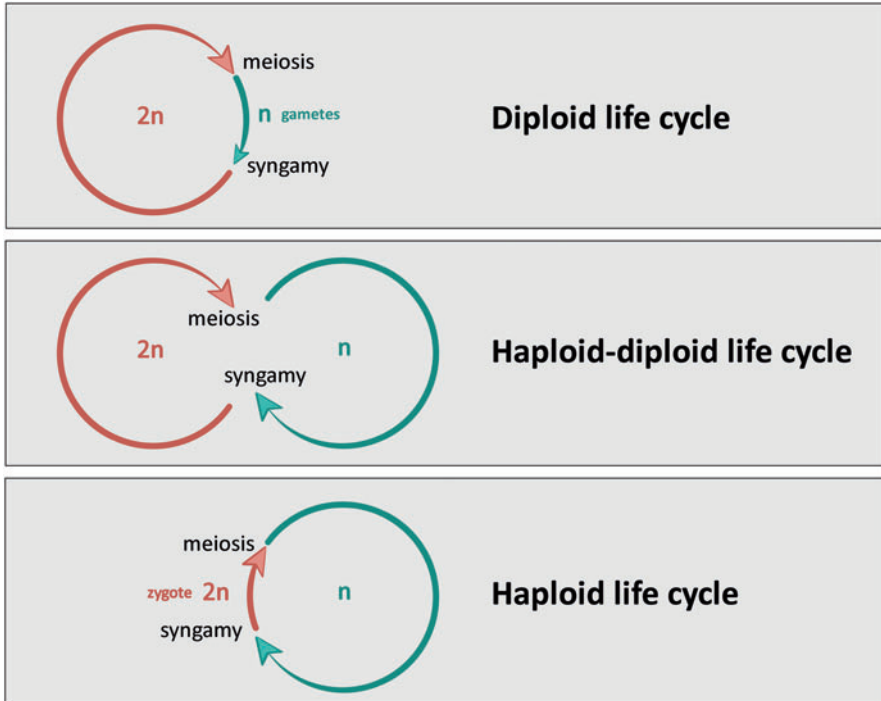


**Fig. 1** Schematic tree of the eukaryotes showing the positions of algal groups. Green lettering indicates groups that include photosynthetic organisms (algae). *LECA* last eukaryotic common ancestor

microalga *Chlamydomonas*). Finally, in some organisms, growth occurs during both the haploid and diploid phases. These organisms are said to have haploid-diploid life cycles. Examples include angiosperms, where the macroscopic plant is the diploid phase and microscopic pollen grains and embryo sacs constitute the haploid phase.

The above paragraph applies to both unicellular and multicellular organisms. For the latter, mitosis serves not only to increase cell number (asexual reproduction) but is also the process that underlies construction of the multicellular body plan (development). Multicellular organisms with haploid-diploid life cycles have two multicellular generations. For plants and algae, these two generations are called the sporophyte and the gametophyte, i.e., the spore-producing “plant” (where meiosis occurs to produce spores) and the gamete-producing “plant” (i.e., which generates the gametes), respectively. For these organisms, the alteration of generations referred to in the title of this chapter is the repeated cycle of sporophyte and gametophyte generations produced as a haploid-diploid life cycle progresses.

This chapter will summarize current knowledge about the evolutionary origins and evolutionary trajectories of plant and algal life cycles. We will provide an



**Fig. 2** Main types of sexual life cycle found in eukaryotes. Differences between eukaryotic sexual life cycles depend principally on two key events, meiosis, and gamete fusion (syngamy). The relative positioning of these events determine if the organism spends the majority of its time in the diploid phase (i.e., has a diploid life cycle) or in the haploid phase (i.e., has a haploid life cycle). Many organisms have intermediate life cycles with two generations, one that is haploid and the other diploid (haploid-diploid life cycles)

overview of the different types of life cycle in the major algal groups, look at evolutionary trends within each group and will attempt to relate these trends to theoretical predictions. We will also describe recent advances in understanding how life cycles are controlled at the genetic and epigenetic levels.

## The Diversity of Plant and Algal Life Cycles

The phylogenetic group that includes the green algae and terrestrial plants, the Viridiplantae, consists of two main taxa, the chlorophytes and the streptophytes (Leliaert et al. 2012; Fig. 1). Most chlorophytes have haploid life cycles (e.g., the unicellular alga *Chlamydomonas*), but some taxa with multicellular members exhibit haploid-diploid life cycles. The haploid-diploid life cycles of multicellular chlorophyte algae can either involve an alternation between morphologically similar generations (i.e., isomorphic life cycles, e.g., *Ulva*) or the two generations can be

morphologically dissimilar (i.e., heteromorphic life cycles). Clear evolutionary trends are difficult to discern within this group because individual sub-taxa can exhibit highly diverse morphologies and because there is still some uncertainty about the phylogenetic relationships between groups within the chlorophytes. In contrast, within the streptophytes, there has been a clear general trend toward increased multicellular complexity and dominance of the diploid phase of the life cycle. The common ancestor of the streptophytes was probably a unicellular organism with a haploid life cycle. The diversification of the charophytes saw an increase in the complexity of the haploid phase with the emergence of a complex, multicellular haploid generation. The shift from haploid-dominated to diploid-dominated life cycles began when the embryophytes emerged from within the charophytes, with the acquisition of a multicellular diploid generation that tended to increase in complexity as new taxa emerged through evolutionary time.

The red algae include both unicellular and multicellular species, but sexual cycles have not been described for the unicellular species. With the exception of some filamentous species, most multicellular red algae belong to one of the two most recently evolved classes within the red algae, the Bangiophyceae or the Florideophyceae. All of the species in these two classes have haploid-diploid life cycles, although the detailed structure of the life cycle can be quite complicated. The edible seaweed *Pyropia yezoensis* (formerly *Porphyra yezoensis*), a member of the Bangiophyceae, alternates between a leaflike gametophyte and a microscopic, filamentous sporophyte generation. The majority of florideophytes have complex “triphasic” life cycles, with what can be considered to be two sporophyte generations. Gamete fusion occurs on the female gametophyte, and the zygote grows to form the first sporophyte generation (the cystocarp), a small “organism” that grows parasitically on the gametophyte. The cystocarp releases spores that develop into the second, free-living sporophyte generation (the tetrasporophyte), on which meiosis occurs when mature. Such triphasic life cycles can be considered to be variants on the standard haploid-diploid life cycle; the two sporophyte stages serve to multiply this generation of the life cycle.

The brown algae (Phaeophyceae) have diverse life cycles ranging from haploid-diploid life cycles (with various levels of dominance of the haploid and diploid phases) to simple diploid life cycles (Bell 1997; Cock et al. 2013). Basal brown algal lineages all have haploid-diploid life cycles, suggesting that the last common ancestor of the brown algae also had a life cycle of this type (Silberfeld et al. 2010). The most developmentally complex brown algae are found in recently evolved orders such as the Laminariales (kelps) and the Fucales, and there is marked tendency within these orders for the diploid phase to be the dominant phase of the life cycle. For example, the large thalli of kelps, which can attain up to 50 meters in length in some species, correspond to the sporophyte generation while kelp gametophytes are microscopic, filamentous organisms. On the other hand, the Ectocarpales, which are the sister order to the kelps, tend to be less developmentally complex and exhibit diverse haploid-diploid life cycles that include both haploid- and diploid-dominant cycles (i.e., cycles with two generations but with one generation larger than the other). The Fucales, which originated about 52–80 Mya (Kawai

et al. 2015) and have relatively large, complex thalli, have diploid life cycles. Hence, although perhaps not as strongly marked as in the archaeplastid lineage, there appears to be a tendency within the brown algae for diploid-dominant life cycles to have been associated with the emergence of developmental complexity.

With the recent availability of well-supported phylogenies for the brown algae (Silberfeld et al. 2010; Kawai et al. 2015), it has become clear that there has been considerable switching between life cycle types over the course of the emergence of this lineage (Cock et al. 2013). The brown algae therefore potentially represent an interesting group in which to correlate life cycle structure with other parameters such as environmental and ecological context.

Algae in other eukaryotic supergroups also exhibit various types of life cycle, with, for example, most dinoflagellates having haploid life cycles and the occurrence of haploid-diploid life cycles in the chlorarachniophytes, but the sexual life cycles of many of these algae are unknown.

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## **A Relationship Between Life Cycle Type and Degree of Multicellular Complexity**

If we focus on the two most developmentally complex eukaryotic lineages, the land plants and the animals, there appears to be a strong correlation between dominance of the diploid phase of the life cycle and the emergence of developmental complexity. As mentioned above, the emergence of land plants corresponded to a gradual reduction in the importance of the gametophyte generation and an increase in the relative importance of the sporophyte. In animals, dominance of the diploid phase was established very early, with the vast majority of these organisms having diploid life cycles. There is also some evidence for a similar correlation in brown algae (the third most complex group of multicellular organisms), with recently evolved, developmentally complex taxa showing a tendency toward diploid-dominant haploid-diploid life cycles or diploid life cycles. No clear trend is observed in other multicellular groups such as the red algae, but this may be because these organisms exhibit lower levels of developmental complexity.

In order to understand the relationship between life cycle structure and the evolution of multicellular complexity, it is important to take into account the possible theoretical advantages and disadvantages of different types of life cycle. These aspects are discussed in the following section (see Otto and Gerstein 2008 and Coelho et al. 2007 and references therein for further details).

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## **Theoretical Advantages and Disadvantages of Different Types of Life Cycle**

It has been proposed that diploid genomes may be advantageous in a number of respects. The presence of two copies of each chromosome can result in masking of recessive deleterious mutations, reducing the negative effects of mutations. Also,

more genes are present, increasing the probability of advantageous mutations arising. Diploidy may also be important for long-lived multicellular organisms that have to deal with rapidly evolving parasites in that a larger battery of alleles is available to provide resistance. Also, because cell size is often correlated with ploidy, it may be advantageous to be diploid if large cells are required (or, conversely, haploid if small cells are advantageous). On a more mechanistic level, the presence of homologous chromosomes in diploids provides a template for the repair of double-stranded DNA breaks. Some of these proposed advantages, such as increased cell size or a possible increased capacity to resist parasites, may be relevant to the emergence of complex multicellularity.

As far as haploid genomes are concerned, while masking of deleterious mutations in diploid genomes may be an advantage in the short term, the more effective elimination of deleterious mutations from haploid genomes due to the absence of masking may be advantageous in the long term. Similarly, although advantageous mutations may have a lower probability of arising in a haploid (because there are fewer gene copies), recessive advantageous mutations will be immediately beneficial. Haploid genomes could also have an energetic advantage, as less resources are required to replicate a smaller genome.

While these different advantages and disadvantages may help explain the dominance of either diploid or haploid life cycles, they do not provide any explanation for the emergence (or evolutionary stability) of haploid-diploid life cycles. A possible advantage of haploid-diploid life cycles is that they reduce the cost of sex (because sexual reproduction occurs over a period of two generations rather than one). However, the cost of sex can also be reduced by increasing the amount of asexual reproduction. Most attempts to explain the prevalence and stability of haploid-diploid life cycles have concentrated on ecological considerations. Such a life cycle may be advantageous, for example, if the two phases are able to exploit different ecological niches, particularly if environmental conditions are variable. Here “environmental conditions” can be understood in a broad sense, not only in terms of the physical environment but also in terms of interactions with other organisms within the ecosystem. For example, if the two phases of the life cycle have different levels of susceptibility to a particular pathogen, life cycle alternation could allow the organism to “escape” from an infection (the so-called Cheshire cat strategy; Frada et al. 2008). Note that, while these hypotheses may explain the existence of two generations, they do not explain why the two generations should have different levels of ploidy. It has been proposed that, in some instances, alternation between two generations may allow one generation to be optimized for spore production (favoring dissemination) and the other for gamete production (favoring gamete fusion) (Bell 1997), but this hypothesis is unlikely to apply to all cases, particularly for isomorphic life cycles for example. It is possible, however, that the level of ploidy of each generation is irrelevant and the main role of the life cycle in these instances is to ensure a cyclic alternation between the two different generations. In other words, in situations where it is advantageous for an organism to alternate between two different forms, the pre-existing alternation between haploid

and diploid phases, inherent to all life cycles, may provide a good starting point for the evolution of the two alternating variant forms.

A number of studies have attempted to test the predictions of the various hypotheses discussed above (Otto and Gerstein 2008). For example, there is evidence for unicellular organisms that masking of deleterious mutations in diploids can make them better adapted to a mutagenic environment (but see below for multicellular organisms). Similarly, haploid life cycles appear to be advantageous if population sizes are large because more mutations tend to arise in the population, but selection is limiting. As far as haploid-diploid life cycles are concerned, the ecological roles of the two generations have also been studied for a number of taxa across the different algal groups. For heteromorphic cycles, where the sporophyte and gametophyte are morphologically different, the differences between the ecological roles of each generation can be quite evident. However, even for isomorphic haploid-diploid life cycles, where the sporophyte and gametophyte are morphologically similar, there are often subtle differences between the two generations that result in them being better adapted to different niches.

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## Genetic Regulation of Life Cycle Transitions

In multicellular organisms it is crucial that the initiation and progress of multicellular development be coordinated with the life cycle. Indeed, initiation of developmental processes at the wrong stage of the life cycle could have catastrophic consequences. The regulatory link between life cycle and development is still poorly understood, but there have been some important advances over the last decade. When considering such systems, one obvious starting hypothesis is that the regulation of development during the life cycle involves some sort of system that senses the level of ploidy (DNA content) of the cell. However, there is currently no evidence to support such a mechanism. For example, it has been shown for several different organisms that experimental modifications of ploidy, such as the creation of tetraploids, do not necessarily disrupt coupling between life cycle progression and development. These observations indicated that the coupling of life cycle and development is more likely under genetic control. Moreover, given that the different stages of a life cycle are all produced from the same genome, the genetic components are expected to be influenced by, and integrated with, epigenetic regulatory processes.

Genetic analyses of several organisms have identified key regulators associated with syngamy (the step of the life cycle where gametes fuse to create a zygote leading to a doubling of the chromosome number) (Goodenough and Heitman 2014; Bowman et al. 2016). The green alga *Chlamydomonas reinhardtii*, for example, produces gametes of two different mating types, called plus and minus gametes (Fig. 3a). Two different three-amino acid length extension (TALE) homeodomain transcription factors (TALE HD TFs) called gamete-specific plus 1 (GSP1) and gamete-specific minus 1 (GSM1) are expressed specifically in the plus and minus gametes, respectively. When a plus and a minus gamete fuse, during syngamy, these two transcription factors are brought together in the same cell, the zygote. In the



zygote, GSP1 and GSM1 form a heterodimer, which orchestrates the expression of processes associated with the diploid phase of the life cycle (Lee et al. 2008). Therefore, in *C. reinhardtii*, a simple genetic system allows the cell to detect when there has been a transition from the haploid to the diploid state.

A similar system has been identified in the moss *Physcomitrella patens* (Sakakibara et al. 2013; Horst et al. 2016). The *C. reinhardtii* proteins GSP1 and GSM1 are members of the BELL and KNOX2 classes of TALE HD TFs, respectively. Analysis of a *P. patens* strain carrying mutations in two KNOX2 TALE HD TF genes, *PpMKN1* and *PpMKN6*, showed that it produced a diploid gametophyte instead of the sporophyte stage of the life cycle (Sakakibara et al. 2013). Similarly, overexpression of the BELL TALE HD TF gene *PpBELL1* resulted in apogamous sporophytes (i.e., the production of haploid sporophytes without syngamy) (Horst et al. 2016).

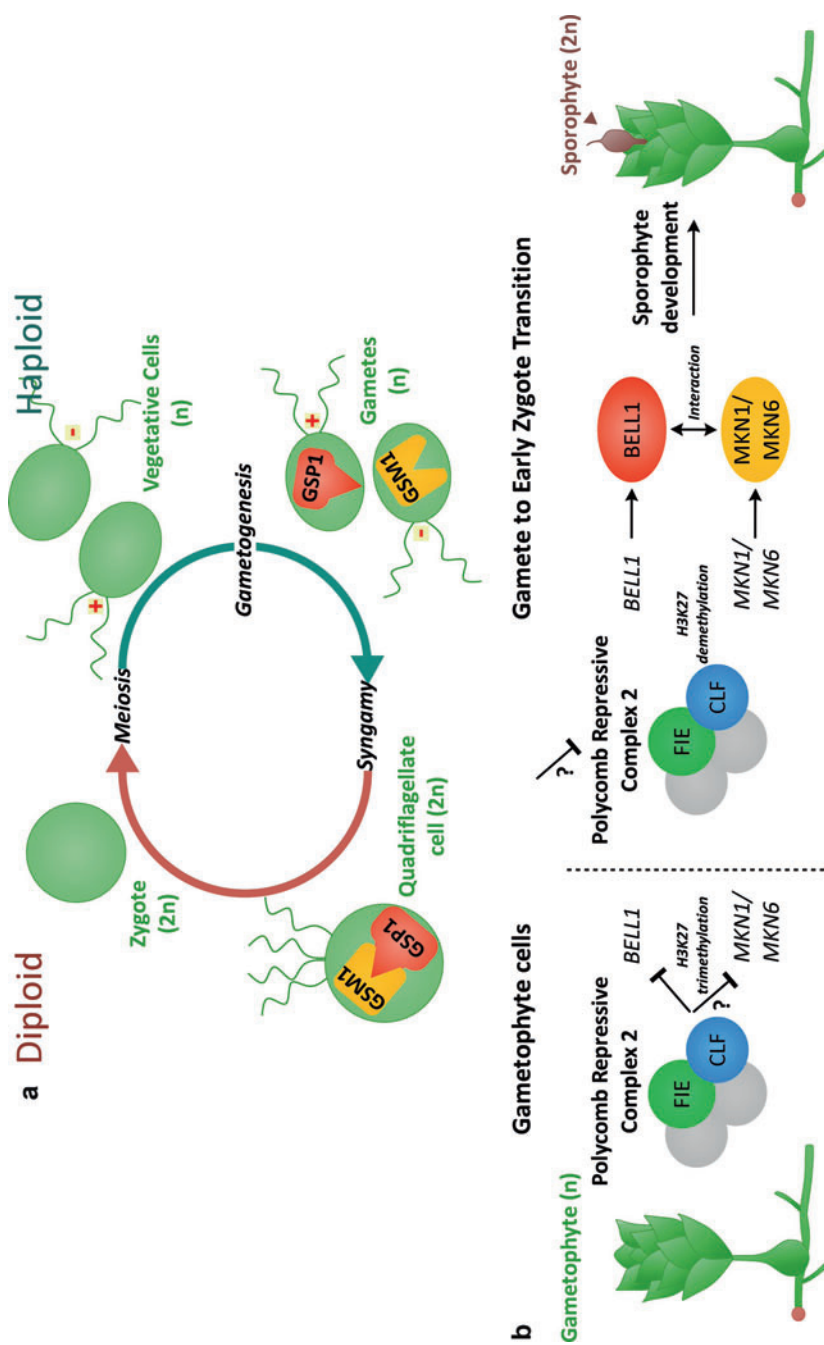
Interestingly, similar molecular systems have been described in another eukaryotic supergroup, the fungi. In *Cryptococcus neoformans*, for example, gametes of the  $\alpha$  and *a* mating types express two different homeodomain transcription factors, sex-inducer 1 $\alpha$  and sex-inducer 2a, respectively. These transcription factors form a heterodimer in the zygote and trigger sexual development, including basidium and meiospore formation (Hull et al. 2005). There is therefore a recurring theme of association of homeodomain transcription factors with the regulation of key life cycle transitions across diverse eukaryotic supergroups. It is not clear at present whether these similarities represent convergent evolution or if the different homeodomain-based regulatory systems are derived from a common, ancestral system that would therefore date back to the last eukaryotic common ancestor (LECA; Fig. 1).

There is also direct genetic evidence for the involvement of epigenetic processes in life cycle control. In *P. patens*, for example, knockout experiments indicate that *curly leaf* (*PpCLF*) and *fertilization-independent endosperm* (*PpFIE*), which are components of the chromatin-regulating polycomb repressive complex 2 (PRC2), downregulate the expression of *PpBELL1* during the gametophyte stage by trimethylating lysine 27 of histone H3 (H3K27me3) in nucleosomes at the *PpBELL1* locus (Pereman et al. 2016). PRC2 proteins are not expressed in the zygote after syngamy, and upregulation of *PpBELL1* leads to the development of the sporophyte generation, presumably through an interaction with *PpMKN1* and *PpMKN6* (Okano et al. 2009; Horst et al. 2016) (Fig. 3b).

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## The Origins of Sporophyte and Gametophyte Developmental Programs

To understand the emergence of multicellular complexity, it is often very important to take into consideration the context of the life cycle. In the land plants, for example, the increase in developmental complexity over evolutionary time was associated with a transition from dominance of the haploid phase to dominance of the diploid phase (Pires and Dolan 2012). There has been considerable debate as to whether the



**Fig. 3** Molecular regulators of life cycle progression. **(a)** The life cycle of the unicellular green alga *Chlamydomonas reinhardtii* showing the expression of the TALE homeodomain transcription factors GSP1 and GSM1 in plus and minus gametes, respectively, and the formation of a GSP1/GSM1 heterodimer after

emergence of the sporophyte generation in this lineage involved de novo evolution of developmental pathways (the so-called “antithetic” hypothesis), or whether the developmental plan was an adapted version of the gametophyte program (the “homologous” hypothesis). Genomic approaches are starting to resolve this question, and the emerging picture is that recruitment of regulatory networks from the gametophyte generation played a very important role in this process, although there have also been sporophyte-specific innovations such as the employment of TALE homeodomain transcription factors of the KNOX2 family as developmental regulators.

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### Consequences of Life Cycle Type on Genome Evolution

The life cycle of an organism is expected to have consequences for the evolution of its genome. For example, in organisms with haploid-diploid life cycles, selection should act more efficiently on genes expressed during the haploid phase because recessive alleles of genes that are expressed during the diploid phase can be masked by dominant alleles that are also present in the diploid genome (Otto and Gerstein 2008). There is evidence that this phenomenon of masking occurs in unicellular organisms, but, surprisingly, it may not play an important role in multicellular organisms. A recent analysis of two land plant species with haploid-diploid life cycles, the angiosperm *Arabidopsis thaliana* and the moss *Funaria hygrometrica*, did not find any evidence that diploid phase-specific genes evolved more rapidly than haploid-phase-specific genes (Szovenyi et al. 2013). In fact, the evolution of life cycle-regulated genes was found to be influenced more strongly by another factor: breadth of expression. The strength of selection on a gene sequence is related to its pattern of expression because a gene that is expressed in multiple tissues and at multiple stages of development is exposed to selection more sustainedly than a gene with a very restricted pattern of expression. In land plants at least, this phenomenon appears to influence the evolution of life cycle-regulated genes more strongly than the masking effect.



**Fig. 3** (continued) gamete fusion. **(b)** Regulators of the gametophyte-to-sporophyte transition in the moss *Physcomitrella patens*. *Left* panel: The polycomb repressive complex (PRC2) represses expression of the TALE homeodomain transcription factor BELL1 (and MKN1/MKN6?) during the gametophyte generation by laying down a repressive chromatin mark. *Right* panel: BELL1 and MKN1/MKN6 are required for initiation of the sporophyte program, and this process probably involves the formation of transcription factor heterodimers. Proteins are indicated by *colored shapes*. Genes are indicated by *italics*

## Conclusion

In this chapter, we have seen that plant and algal life cycles are highly varied and often very complex. As far as the emergence of multicellularity is concerned, there appears to be a correlation between the dominance of the diploid phase and multicellular complexity, at least in the most developmentally complex groups such as animals, land plants, and brown algae. The diversity of algae provides a rich source of variation to test theoretical predictions about the relative advantages of different types of life cycle. Algal systems are also providing exciting new insights into the molecular mechanisms regulating life cycle progression and the evolutionary processes that have led to the emergence of the sporophyte and gametophyte generations of the life cycle. These various themes illustrate the importance of life cycles as key processes underlying important evolutionary transitions, including adaptations to new environments and the evolution of multicellular complexity.

## Glossary

<i>Alga</i>	Photosynthetic eukaryotes, other than land plants
<i>Diploid</i>	Phase of the life cycle with two sets of chromosomes
<i>Epigenetic</i>	A change in gene expression that is not due to modification of the DNA sequence of the genome
<i>Gametophyte</i>	The gamete-producing generation of a plant or algal life cycle
<i>Generation</i>	The organism produced at each stage of a life cycle. We use generation here to distinguish morphological/functional stages of the life cycle such as the sporophyte and the gametophyte from the ploidy phases (haploid and diploid phases)
<i>Haploid</i>	Phase of the life cycle with a single set of chromosomes
<i>Haplodiploidy</i>	Sometimes used as a synonym for haploid-diploid life cycles, but this term can lead to confusion because it is also used to describe Hymenoptera life cycles that involve development of haploid males from unfertilized eggs and diploid females from fertilized eggs (also called arrhenotoky)
<i>Meiosis</i>	Cell division process that results in daughter cells that contain half as many chromosomes as the parent cells. Recombination between chromosomes during meiosis generates new combinations of alleles in the chromosomes of the daughter cells
<i>Phase</i>	Stage of a life cycle with a specific level of ploidy, e.g., the diploid or the haploid phase
<i>Plant</i>	Macroscopic photosynthetic eukaryote. When used in a taxonomic sense, this term refers to a member of the

	kingdom Plantae, equivalent to the modern taxonomic group the Archaeplastida (Fig. 1)
<i>Primary endosymbiosis</i>	Capture of a cyanobacterium by a eukaryotic cell and enslavement to form a plastid
<i>Secondary endosymbiosis</i>	Capture and enslavement of a photosynthetic eukaryote by another eukaryotic cell leading to the production of a secondary plastid
<i>Sporophyte</i>	The spore-producing generation of a plant or algal life cycle
<i>Syngamy</i>	Fusion of gametes leading to doubling of the chromosome number in the resulting zygote

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