

Alternation of haploid and diploid generations: evolution by gamete amplification

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ABSTRACT

Question: What selects for the alternation of haploid and diploid generations in algal taxa?

Mathematical methods: We derive the growth rates of haplontic, diplontic, and haplo-diplontic populations as functions of ploidy-dependent survival probabilities and propagule production rates. We use a population genetic model with a single locus coding for haplonty, diplonty, and haplo-diplonty to obtain the evolutionarily stable conditions for the fixation of each of the three ploidy-cycles. We simulate the evolutionary dynamics to demonstrate the convergence to these equilibria.

Key assumptions: Non-overlapping generations, ploidy-dependent propagule production and survival rates, and the synchronous release of gametes into water by the entire population. We assume that the fertilization probability of eggs increases as a function of the sperm density encountered.

Conclusions: The ploidy-cycle selected is predicted to be the one with the highest population growth rate defined by propagule production and survival rates. Haplo-diplonty may be selected in low fertilization environments because it mitigates the problem of sperm limitation, as the gamete concentration amplifies over subsequent generations. Diplonty may be favoured in more variable environments because diploidy confers higher viability in such environments.

Keywords: algae, alternation of generations, fertilization probability, haplo-diplonty, ploidy, sperm limitation.

INTRODUCTION

The sexual cycle in most organisms involves both haploid and diploid cells (e.g. gametes and zygotes). In most multicellular species, either haploid or diploid cells constitute the multicellular individual; cells of the other ploidy are unicellular. In contrast, many species of algae, fungi, and plants show an alternation of haploid and diploid multicellular generations (Bell, 1994), and are called haplo-diplontic (Richerd *et al.*, 1993). The haploid phase of a haplo-diplontic species is referred to as the gametophyte and the diploid phase as the sporophyte. In some haplo-diplontic species, one of these generations is much reduced and dependent on the other generation; as an extreme example, the two-celled pollen grain

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and the seven-celled megagametophyte constitute the male and female gametophytes of seed plants. The two generations in the other species are free living and independent of each other, and may be either morphologically identical (isomorphic) or different (heteromorphic). Although many of the models discussed below have proposed advantages to haplonty and diplonty, identifying the factors leading to the evolutionary stability of haplo-diplonty remains a problem (Valero *et al.*, 1992).

Genetic hypotheses for the evolution of haplo-diplonty include the effect of ploidy on the masking and elimination of deleterious mutations. While diploids may be better at masking these mutations and haploids at eliminating them, models find that the balance of these two forces selects for either haplonty or diplonty (Kondrashov and Crow, 1991; Perrot *et al.*, 1991; Otto and Goldstein, 1992; Otto and Marks, 1996), but not for haplo-diplonty (Jenkins and Kirkpatrick, 1994, 1995). Other models suggest that beneficial mutations occur with higher probabilities in diploids, but they increase to fixation faster in haploids, the actual fixation speed depending on the rate of recombination. Again, either haplonty or diplonty is favoured, but not haplo-diplonty (Orr and Otto, 1994).

A second class of models focuses on the life-history differences between the haploid and diploid individuals of a haplo-diplontic species. Jenkins (1993) found a constant difference between instantaneous mortality rates in the haploid and diploid phases to be insufficient to select for haplo-diplonty. Hughes and Otto (1999) demonstrated that small demographic differences between the haploid and diploid individuals may be sufficient to render haplo-diplonty evolutionarily stable. However, their model does not explain the link between ploidy and the selection for different life-history traits. Moreover, a polymorphism in life-history traits may be maintained even without an alternation of ploidy generations (Klinger, 1993; Bell, 1994).

Richerd *et al.* (1993) suggest that haplo-diplonty may reduce the cost of sex, as sexual reproduction occurs less frequently in haplo-diplontic species, with sexual reproduction occurring only every other generation compared with haplontic or diplontic species, which reproduce sexually every generation. The frequency of sex can also be reduced by vegetative propagation, which is common in many taxa where haplo-diplonty is prevalent. Nevertheless, the reduced frequency of sex necessarily accompanies the alternation of haploid and diploid generations, and is a factor we incorporate into our own model.

Apart from the reduced cost of sex, the lower frequency of sexual reproduction also implies that haplo-diplonts face the risk of having their eggs not fertilized less often. In this paper, we focus on algae – species that broadcast their sperm (and often eggs) into water, and hence are often sperm limited (Levitan, 1996; Levitan and Petersen, 1995). Alternation of generations could be selected as an adaptation to sperm limitation because the spores produced by the sporophytic generation do not need fertilization. Consequently, compared with haplonts or diplonts whose gametes need to be fertilized every generation, haplo-diplonts may have a higher growth rate. Furthermore, the higher growth rate may also result in an amplification of the gamete density, and hence the fertilization probability, between generations. Hence, the gametophytic generation can be viewed as a structure produced by a gamete (spore), which in turn makes more gametes – thus increasing the gamete's presence in the gamete pool in both space and time by delaying the generation at which fertilization occurs. These ideas suggest a novel hypothesis for the selection of haplo-diplonty – under conditions of sperm limitation, populations with alternating haploid and diploid generations have a higher growth rate than haplontic or diplontic populations.

In the rest of the paper, we use the word 'propagule' to refer to both spores and zygotes –

the cells that are often dispersed to initiate a new generation. While the alternation of generations may increase propagule production under conditions of sperm limitation, propagule survival to adulthood is expected to depend on its ploidy. By virtue of possessing two copies of each gene, diploids have an increased genetic variation, which may enable a higher likelihood of survival over multiple environments. We formalize these ideas in the next section within general frameworks for the population dynamics and evolutionary dynamics for the life-cycles.

MODEL

To understand the fundamental differences between the haplontic, diplontic, and haplo-diplontic life-cycles in terms of the effects of the life-history parameters on the population growth rates, we first consider separate populations of haplontic, diplontic, and haplo-diplontic species. Once we derive the conditions for each population to have a higher growth rate than the other two, we consider a population genetic model for an inter-breeding population of haplonts, diplonts, and haplo-diplonts. We find that the condition for the evolutionary stability of each life history is the same as the condition for the corresponding single life-cycle population to have the highest growth rate. Finally, we simulate the evolutionary dynamics to show that they do indeed converge to the evolutionarily stable equilibria.

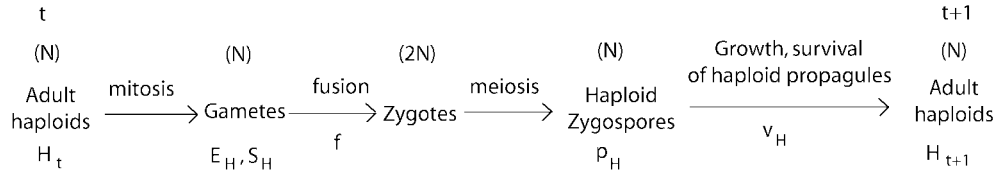
Population growth rates

The haplontic life-cycle consists of adult haplonts that produce eggs and sperm. The resulting zygote immediately undergoes meiosis to make haploid zygospores, the propagules that develop to constitute the next adult generation. The diplontic life-cycle is similar with diploid adults producing eggs and sperm. The fertilized zygotes then germinate to produce the diploid adults. The gametophytes of the haplo-diplontic species make gametes (eggs and sperm), which undergo fertilization to form zygotes. The zygotes germinate to form the diploid sporophytic plants, which produce haploid spores by meiosis. The spores in turn germinate into gametophytic adults without undergoing fertilization. The three life-cycles are summarized in Fig. 1. While most diplontic and haplo-diplontic zygotes of green and brown algal species directly mature into diploid adults, the red algae are characterized by the production of numerous diploid carpospores from a single zygote. To include this variation in life history, and for symmetry with the haplontic life-cycle, our framework assumes that all zygotes first divide into diploid zygospores that then mature into adults.

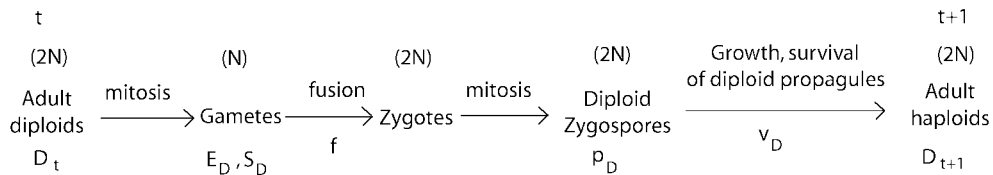
We can infer from the schematic that the life-history parameters relevant to calculating the growth rates are the number of propagules produced and the survival probability of these propagules to adulthood. We assume that the generations are non-overlapping, hence all adults in each generation arise from propagules produced by the previous generation.

One may expect from familiarity with the haplontic and diplontic life-cycles that the haplo-diplontic life-cycle consists of an alternation between strictly haploid and strictly diploid life-cycles, such that adults in the haploid phase produce gametes whose zygotes mature into the diploid adults, and the diploid adults also produce gametes, which undergo meiosis soon after fertilization to form the haplospores that mature into the haploid adults. However, such a life-cycle is unknown in nature, and the haplo-diplontic life-cycle instead involves sexual reproduction and fertilization only in the gametophytic stage, as in Fig. 1.

(A) Haplontic life-cycle



(B) Diplontic life-cycle



(C) Haplo-diplontic life-cycle

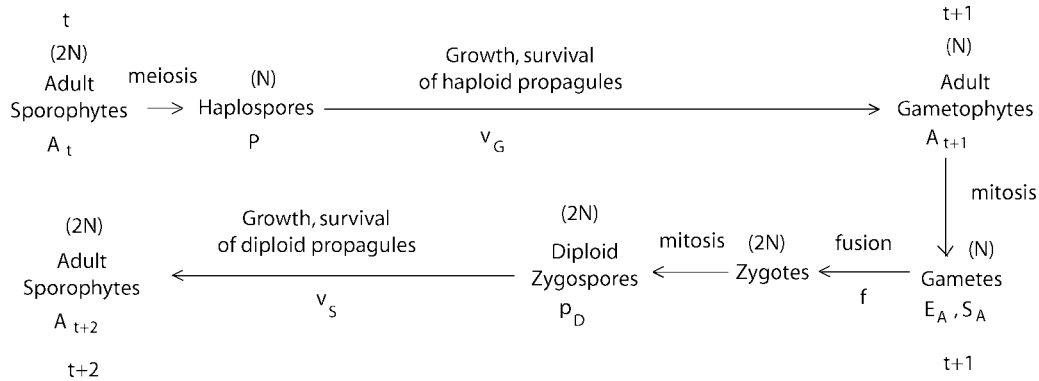


Fig. 1. Comparison of (A) haplontic, (B) diplontic, and (C) haplo-diplontic life-cycles.

This is consistent with the theoretical predictions because a strict alternation between haplonty and diplonty would confer a fitness intermediate to that of haplonts and diplonts, and hence would never be selected over haplonty or diplonty. Instead, haplo-diplonty is likely selected as a consequence of the alternation of sexual and vegetative generations that distinguishes it from haplonty or diplonty.

To derive the equations for population growth rates, we first consider a population of H_t haplonts. Suppose the population is dioecious, and consists of an equal number of males and females. If each female produces E_H eggs, the $H_t/2$ females produce a total of $H_t E_H/2$ eggs. Similarly, if each male produces S_H sperm and all the $H_t/2$ males release their sperm synchronously, the number of sperm in the gamete pool is $H_t S_H/2$. If this sperm density leads to a probability $f(H_t S_H/2)$ that each egg is fertilized, a total of $H_t E_H/2 f(H_t S_H/2)$ zygotes are produced. f is an increasing function of the amount of sperm in the gamete pool, and saturates at the value 1. For the purposes of deriving the general expressions for

population growth rates, specifying a functional form of f unnecessarily clutters the equations and distracts from the insights. Hence we now stick to the use of an unspecified function f for the fertilization probability, which we later instantiate with the Michaelis-Menton equation ($f(s) = ks/(ks + 1)$) for the simulations.

If each zygote immediately disintegrates into p_H haploid zygospores, which each survive to adulthood with probability v_H , the population size after one generation becomes

$$H_{t+1} = \frac{H_t E_H}{2} f\left(\frac{H_t S_H}{2}\right) p_H v_H$$

and after two generations is

$$H_{t+2} = \frac{H_{t+1} E_H}{2} f\left(\frac{H_{t+1} S_H}{2}\right) p_H v_H = H_t \frac{E_H^2}{4} f\left(\frac{H_t S_H}{2}\right) f\left(\frac{H_{t+1} S_H}{2}\right) p_H^2 v_H^2$$

Now consider a diplontic population of size D_t at generation t . Suppose the sex ratio is 1:1, and each male produces S_D sperm and each female E_D eggs. Hence a total of $D_t E_D/2$ $f(D_t S_D/2)$ zygotes are produced. Suppose each zygote then undergoes mitosis to produce p_D diploid zygospores, each of which survives to adulthood with probability v_D . Then,

$$D_{t+1} = \frac{D_t E_D}{2} f\left(\frac{D_t S_D}{2}\right) p_D v_D$$

and

$$D_{t+2} = \frac{D_{t+1} E_D}{2} f\left(\frac{D_{t+1} S_D}{2}\right) p_D v_D = D_t \frac{E_D^2}{4} f\left(\frac{D_t S_D}{2}\right) f\left(\frac{D_{t+1} S_D}{2}\right) p_D^2 v_D^2$$

Finally, consider a haplo-diplontic population. Suppose this population is sporophytic at generation t , consisting of A_t diploid adults that each produce P haploid spores by meiosis. The spores survive to gametophytic adulthood with probability v_G , without needing to be fertilized. Thus the adult population size after one generation has a different form from that for haplonts or diplonts:

$$A_{t+1} = A_t P v_G$$

Suppose the A_{t+1} gametophytes are equally likely to be male or female, males producing S_A sperm and females E_A eggs. Then the total number of sperm in the sperm pool is $A_{t+1} S_A/2 = A_t P v_G S_A/2$, and leads to a probability $f(A_t P v_G S_A/2)$ that each egg is fertilized. The resulting zygotes undergo mitosis to produce p_D diploid zygospores, which survive to sporophytic adulthood with probability v_S . Hence the population size after two generations is

$$A_{t+2} = \frac{A_{t+1} E_A}{2} f\left(\frac{A_{t+1} S_A}{2}\right) p_D v_S = A_t P v_G \frac{E_A}{2} f\left(\frac{A_t P v_G S_A}{2}\right) p_D v_S.$$

Note the difference in notation between P denoting the number of haploid spores produced by a sporophytic adult, and p_H or p_D for the numbers of haploid or diploid

zygospores produced by each zygote. Typically, the diplontic and haplo-diplontic zygotes of green and brown algae do not undergo mitosis ($p_D = p_A = 1$), while the haplontic zygotes undergo meiosis once ($p_H = 4$).

Hence we can calculate the growth rates of the three populations over two generations to be:

$$\begin{aligned} r_H &= \frac{H_{t+2}}{H_t} = \frac{E_H^2}{4} p_H^2 v_H^2 f\left(\frac{H_t S_H}{2}\right) f\left(\frac{H_{t+1} S_H}{2}\right) \\ r_D &= \frac{D_{t+2}}{D_t} = \frac{E_D^2}{4} p_D^2 v_D^2 f\left(\frac{D_t S_D}{2}\right) f\left(\frac{D_{t+1} S_D}{2}\right) \\ r_A &= \frac{A_{t+2}}{A_t} = P \frac{E_A}{2} p_D v_G v_S f\left(\frac{A_t P v_G S_A}{2}\right) \end{aligned} \quad (1)$$

In the case that the survival probability depends only on ploidy ($v_G = v_H$, $v_S = v_D$) and when all females produce the same number of eggs ($E_H = E_D = E_A = E$), the relative population growth rates are:

$$\begin{aligned} r_H &\propto \frac{E}{2} f(\bullet) f(\bullet_{t+1}) p_H^2 v_H^2 \\ r_D &\propto \frac{E}{2} f(\bullet) f(\bullet_{t+1}) p_D^2 v_D^2 \\ r_A &\propto P f(\bullet_{t+1}) p_D v_D v_H \end{aligned} \quad (2)$$

where $f(\bullet)$ refers to the fertilization probability as a function of the number of sperm in the gamete pool at time t .

Equations (2) capture the fundamental differences between the three life histories. The form of r_A is different from r_H and r_D because haplo-diplonts undergo sexual reproduction only every other generation, interspersed by a generation of asexual reproduction. Consequently, haplo-diplonts also avoid the risk of their eggs remaining unfertilized every other generation. Hence if the fertilization probabilities are similar in the three populations, let's say, equal to F , the growth rates are as follows:

$$\begin{aligned} r_H &\propto \frac{EF}{2} p_H^2 v_H^2 \\ r_D &\propto \frac{EF}{2} p_D^2 v_D^2 \\ r_A &\propto P p_D v_D v_H \end{aligned} \quad (3)$$

These equations clarify the dependence of the growth rates on the number of propagules produced over two generations [$(EF/2)p_H^2$, $(EF/2)p_D^2$ or Pp_D], as well as their survival probabilities. As a result of undergoing sexual reproduction only every other generation, haplo-diplonts increase their propagule production by avoiding multiplication by the factors of a half as well as F . F is less than 1 when the eggs are not ensured fertilization.

Hence haplo-diplonts avoid the likelihood of not being fertilized every other generation when spores are produced vegetatively. The factor of a half arises due to the ‘cost of sex’ – while each sporophyte in the haplo-diplontic population produces P spores, only a half of the adults of any gamete-producing generation are females. Furthermore, when the fertilization probability is not fixed, haplo-diplonts can benefit from a greater increase in $f(\bullet)$ between subsequent generations compared with haplonts or diplonts.

On the other hand, haplonts and diplonts have higher growth rates than haplo-diplonts if the fertilization probabilities are relatively high, or the number of spores (P) produced is relatively small. Diplonts can outcompete haplonts and haplo-diplonts due to a high survival probability v_D , and haplonts can do the same if the product $p_H v_H$ is large. Hence which life-cycle has the maximum growth rate depends on how many propagules are produced, the probability they are fertilized, and the probability they survive to the next generation.

Evolutionary model

Now we consider the evolution of these life-cycle strategies by associating a gene with each life-cycle, and allowing individuals with the different strategies to inter-breed. We use a population genetic model to determine the conditions for evolutionary stability of haplonty, diplonty, and haplo-diplonty, and compare these conditions to the population growth rates obtained above.

Suppose the life-cycle is controlled by a single locus with three alleles (A , D , and H) such that the fixation of A corresponds to haplo-diplonty, D to diplonty, and H to haplonty. Hence AA adults are sporophytes that produce A spores, which in turn become male and female gametophytes. DD adults are diploid males and females, produced by the DD zygotes or zygospores. HH zygotes immediately disintegrate into haploid zygospores with allele H , which germinate to form the male and female haploid adults. Let us assume that heterozygous individuals and zygotes behave as each of the corresponding homozygotes with probability $1/2$. Hence half the AD adults are sporophytes and the other half are diploid males and females. Similarly, half each of the AH and DH zygotes formed immediately undergo meiosis to form A , D , and H haploid zygospores. The other half undergo mitosis to form AH and DH diploid zygospores, which in turn survive to become sporophytes and diploid adults respectively. Figure 2 illustrates the genotypic composition of a population after one and two generations, when initiated with sporophytes with genotype AA , diploid males and female adults with genotype DD , and haploid male and female adults with genotypes A (gametophytes) and H (haplonts). We conclude from the figure that individuals in such a population are sporophytes with genotypes AA , AD , AH , haploid adults with genotypes A , D , H or diploid adults with genotypes DD , DH , AD . Hence the evolutionary dynamics result in changes in the frequencies of these genotypes between one generation and the next, as we proceed to derive (Fig. 3).

Suppose the genotype frequencies among the adults are x_{AA} , x_{DD} , x_{AD} , x_{AH} , x_{DH} , x_H , x_A , and x_D , and the population size is N . Then there are $N(x_{AA} + x_{AD}/2 + x_{AH})$ adults that are sporophytes, $N(x_{DD}/2 + x_{DH}/2 + x_{AD}/4)$ diploid males, $N(x_{DD}/2 + x_{DH}/2 + x_{AD}/4)$ diploid females, and $N(x_A + x_D + x_H)$ gametophytes (half of which are males and half females). For simplicity, we suppose that each female produces E eggs and each male S sperm, although the analysis can also be carried out assuming that each life-cycle produces

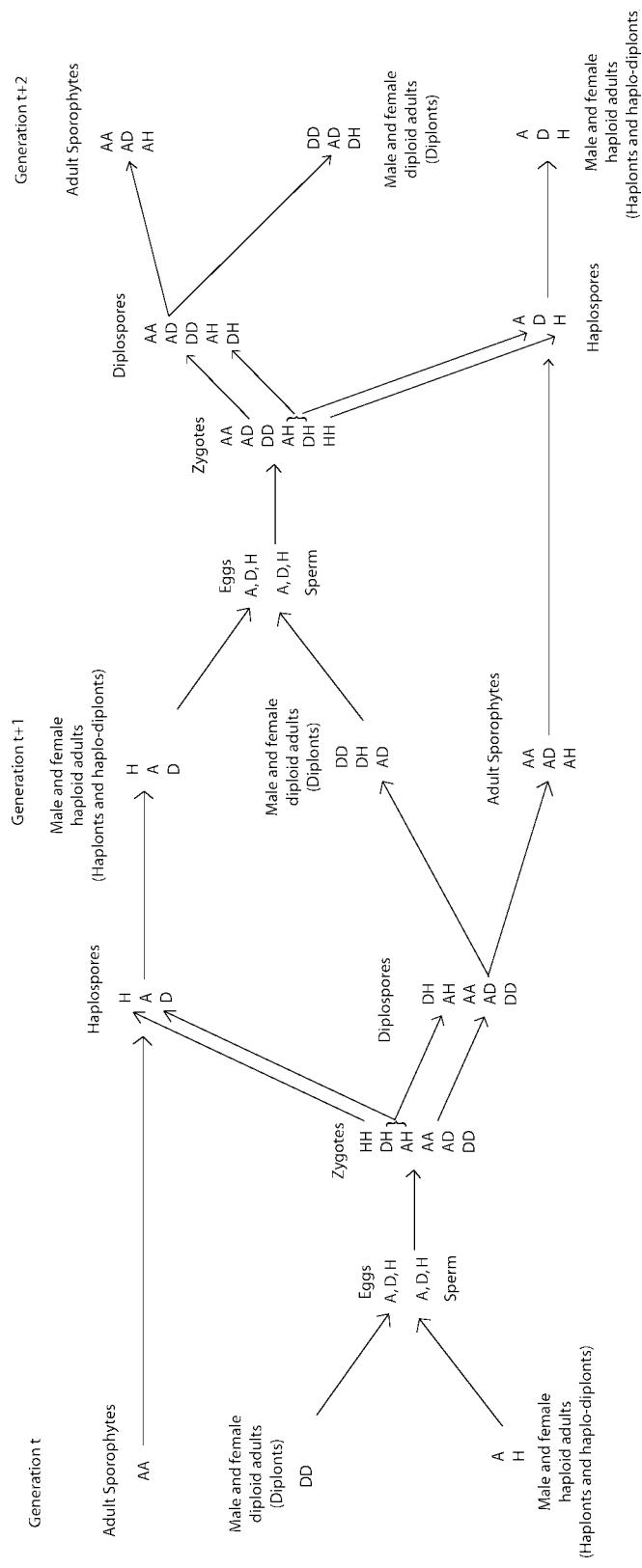


Fig. 2. Changes in genotypic composition over one and two generations.

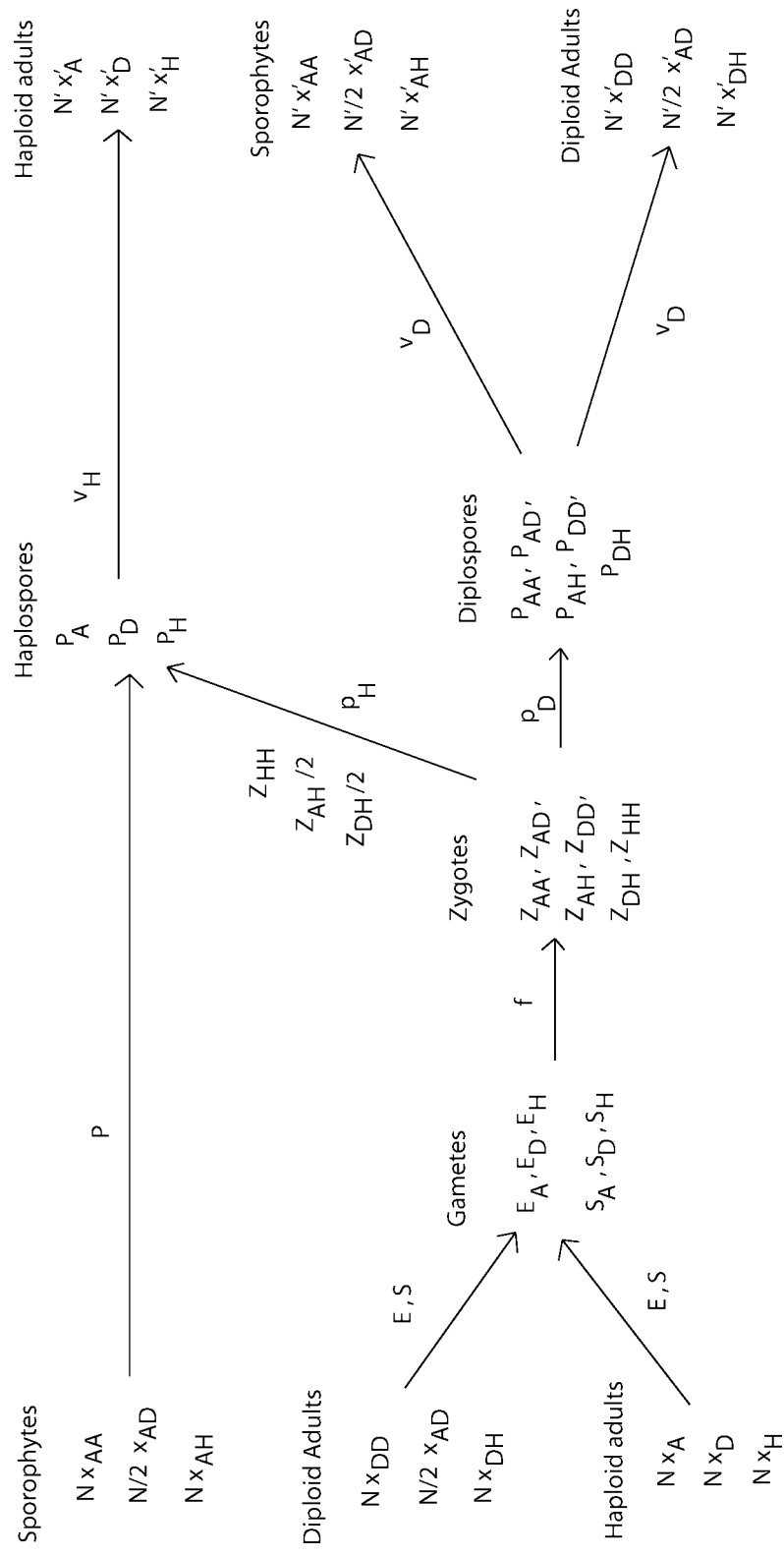


Fig. 3. Transitions in genotype frequencies from one generation to the next.

different numbers of gametes. The number of eggs and sperm of each allele in the gamete pool becomes:

$$\begin{aligned}
 E_A &= EN \left(\frac{x_{AD}}{8} + \frac{x_A}{2} \right) \\
 E_D &= EN \left(\frac{x_{AD}}{8} + \frac{x_D}{2} + \frac{x_{DD}}{2} + \frac{x_{DH}}{4} \right) \\
 E_H &= EN \left(\frac{x_H}{2} + \frac{x_{DH}}{4} \right) \\
 S_A &= SN \left(\frac{x_{AD}}{8} + \frac{x_A}{2} \right) \\
 S_D &= SN \left(\frac{x_{AD}}{8} + \frac{x_D}{2} + \frac{x_{DD}}{2} + \frac{x_{DH}}{4} \right) \\
 S_H &= SN \left(\frac{x_H}{2} + \frac{x_{DH}}{4} \right)
 \end{aligned} \tag{4}$$

The fertilization probability is a saturating function of the total number of sperm in the pool, $f(S_A + S_D + S_H)$, which we denote by $f(\bullet)$. Then the probability that an egg is fertilized by a sperm carrying allele A , for example, is $f(\bullet) S_A / (S_A + S_D + S_H)$. Hence the number of zygotes of each genotype becomes:

$$\begin{aligned}
 Z_{AA} &= \frac{E_A S_A f(\bullet)}{S_A + S_D + S_H} \\
 Z_{AD} &= \frac{(E_A S_D + E_D S_A) f(\bullet)}{S_A + S_D + S_H} \\
 Z_{DD} &= \frac{E_D S_D f(\bullet)}{S_A + S_D + S_H} \\
 Z_{HH} &= \frac{E_H S_H f(\bullet)}{S_A + S_D + S_H} \\
 Z_{AH} &= \frac{(E_A S_H + E_H S_A) f(\bullet)}{S_A + S_D + S_H} \\
 Z_{DH} &= \frac{(E_D S_H + E_H S_D) f(\bullet)}{S_A + S_D + S_H}
 \end{aligned} \tag{5}$$

Haploid spores are produced by sporophytes as well as the zygotes with genotypes HH , AH , and DH . If each zygote divides into p_H spores, the number of spores with each allele is

$$\begin{aligned} P_A &= N \left(x_{AA} + \frac{x_{AD}}{4} + \frac{x_{AH}}{2} \right) P + \frac{Z_{AH}}{4} p_H \\ P_D &= N \frac{x_{AD}}{4} P + \frac{Z_{DH}}{4} p_H \\ P_H &= N \frac{x_{AH}}{2} P + \left(\frac{Z_{AH}}{4} + \frac{Z_{DH}}{4} + Z_{HH} \right) p_H \end{aligned} \quad (6)$$

The other zygotes each divide into p_D diploid zygosporos:

$$\begin{aligned} P_{AA} &= Z_{AA} p_D \\ P_{DD} &= Z_{DD} p_D \\ P_{AD} &= Z_{AD} p_D \\ P_{AH} &= \frac{Z_{AH}}{2} p_D \\ P_{DH} &= \frac{Z_{DH}}{2} p_D \end{aligned} \quad (7)$$

The diploid and haploid spores survive with probabilities v_D and v_H respectively to form the population of adults in the next generation:

$$\begin{aligned} N_{AA} &= P_{AA} v_D \\ N_{AD} &= P_{AD} v_D \\ N_{DD} &= P_{DD} v_D \\ N_{AH} &= P_{AH} v_D \\ N_{DH} &= P_{DH} v_D \\ N_A &= P_A v_H \\ N_D &= P_D v_H \\ N_H &= P_H v_H \end{aligned} \quad (8)$$

By substituting values from equations (3), (4), (5), and (6), and normalizing by the total population size, we obtain the genotype frequencies after one generation:

$$x'_{AA} = \frac{Ef(\bullet) p_D v_D \left(\frac{x_{AD}}{8} + \frac{x_A}{2} \right)^2}{w \left(\frac{x_A}{2} + \frac{x_D}{2} + \frac{x_H}{2} + \frac{x_{AD}}{4} + \frac{x_{DD}}{2} + \frac{x_{DH}}{2} \right)}$$

$$\begin{aligned}
x'_{DD} &= \frac{Ef(\bullet)p_D v_D \left(\frac{x_{AD}}{8} + \frac{x_D}{2} + \frac{x_{DD}}{2} + \frac{x_{DH}}{4} \right)^2}{w \left(\frac{x_A}{2} + \frac{x_D}{2} + \frac{x_H}{2} + \frac{x_{AD}}{4} + \frac{x_{DD}}{2} + \frac{x_{DH}}{2} \right)} \\
x'_{AD} &= \frac{2Ef(\bullet)p_D v_D \left(\frac{x_{AD}}{8} + \frac{x_A}{2} \right) \left(\frac{x_{AD}}{8} + \frac{x_D}{2} + \frac{x_{DD}}{2} + \frac{x_{DH}}{4} \right)}{w \left(\frac{x_A}{2} + \frac{x_D}{2} + \frac{x_H}{2} + \frac{x_{AD}}{4} + \frac{x_{DD}}{2} + \frac{x_{DH}}{2} \right)} \\
x'_{AH} &= \frac{Ef(\bullet)p_D v_D \left(\frac{x_{AD}}{8} + \frac{x_A}{2} \right) \left(\frac{x_H}{2} + \frac{x_{DH}}{4} \right)}{w \left(\frac{x_A}{2} + \frac{x_D}{2} + \frac{x_H}{2} + \frac{x_{AD}}{4} + \frac{x_{DD}}{2} + \frac{x_{DH}}{2} \right)} \\
x'_{DH} &= \frac{Ef(\bullet)p_D v_D \left(\frac{x_{AD}}{8} + \frac{x_D}{2} + \frac{x_{DD}}{2} + \frac{x_{DH}}{4} \right) \left(\frac{x_H}{2} + \frac{x_{DH}}{4} \right)}{w \left(\frac{x_A}{2} + \frac{x_D}{2} + \frac{x_H}{2} + \frac{x_{AD}}{4} + \frac{x_{DD}}{2} + \frac{x_{DH}}{2} \right)} \\
x'_A &= \frac{Pv_H \left(x_{AA} + \frac{x_{AD}}{4} + \frac{x_{AH}}{2} \right)}{w} + \frac{Ef(\bullet)p_H v_H \left(\frac{x_{AD}}{8} + \frac{x_A}{2} \right) \left(\frac{x_H}{2} + \frac{x_{DH}}{4} \right)}{2w \left(\frac{x_A}{2} + \frac{x_D}{2} + \frac{x_H}{2} + \frac{x_{AD}}{4} + \frac{x_{DD}}{2} + \frac{x_{DH}}{2} \right)} \\
x'_D &= \frac{Pv_H \frac{x_{AD}}{4}}{w} + \frac{Ef(\bullet)p_H v_H \left(\frac{x_{AD}}{8} + \frac{x_D}{2} + \frac{x_{DD}}{2} + \frac{x_{DH}}{4} \right) \left(\frac{x_H}{2} + \frac{x_{DH}}{4} \right)}{2w \left(\frac{x_A}{2} + \frac{x_D}{2} + \frac{x_H}{2} + \frac{x_{AD}}{4} + \frac{x_{DD}}{2} + \frac{x_{DH}}{2} \right)} \\
x'_H &= \frac{Pv_H \frac{x_{AH}}{2}}{w} + \frac{Ef(\bullet)p_H v_H \left(\frac{x_H}{2} + \frac{x_{DH}}{4} \right)^2 + \frac{1}{2} \left(\frac{x_{AD}}{4} + \frac{x_D}{2} + \frac{x_{DD}}{2} + \frac{x_{DH}}{4} + \frac{x_A}{2} \right) \left(\frac{x_H}{2} + \frac{x_{DH}}{4} \right)}{w \left(\frac{x_A}{2} + \frac{x_D}{2} + \frac{x_H}{2} + \frac{x_{AD}}{4} + \frac{x_{DD}}{2} + \frac{x_{DH}}{2} \right)} \tag{9}
\end{aligned}$$

where $w = Ef(\bullet)p_D v_A(x_{AD}/8 + x_A/2) + Ef(\bullet)p_D v_D(x_{AD}/8 + x_D/2 + x_{DD}/2 + x_{DH}/4) + Ef(\bullet)p_H v_H(x_H/2 + x_{DH}/4) + Pv_H(x_{AA} + x_{AD}/2 + x_{AH})$.

This is a system of eight equations in eight variables, and is not analytically solvable in general, especially because the function $f(\bullet)$ can take arbitrary saturating forms. Instead, we first consider the conditions for evolutionary stability of the fixation of each of the three alleles, and show that these conditions correspond to the corresponding life-cycle to have the maximum population growth rate as in equations (2). We then simulate the dynamics of genotype frequency change, allowing the fertilization probability to increase with sperm concentration, and demonstrate convergence to the evolutionarily stable strategies.

Conditions for evolutionary stability

In this section, we consider populations with each of the three alleles, A , D and H fixed, and examine the conditions for each of them to be stable to invasions by the other two alleles. The assumption that permits the evolutionary stability analysis of these populations is that the fertilization probability is a constant for a population in equilibrium. This is because the population growth can either be unconstrained to an extent that the population size is large enough for the fertilization probability to be effectively equal to 1, irrespective of the life-cycles present in the population; or, the number of individuals, and hence the number of sperm in the gamete pool, can be limited by constraints that determine the equilibrium population size. This in turn sets the equilibrium fertilization probability in haplontic and diplontic populations to be equal to the value of $f(S)$ evaluated at the sperm concentration S attained at the equilibrium. In the next section, we show that a haplo-diplontic population of a finite size eventually always alternates synchronously between the gametophytic and sporophytic generations. Hence the fertilization probability at any generation where fertilizations occur eventually becomes a constant, and is equal to the same value as the equilibrium fertilization probability for a haplontic or diplontic population of the same size. In the following analysis, we call this constant fertilization probability the population eventually attains f_0 .

Consider first the case that diplonty is initially fixed in the population, hence all individuals have the genotype DD . Suppose a small fraction of the population randomly mutates into gametophytes with genotype A , so $x_A = \varepsilon$ and $x_{DD} = 1 - \varepsilon$. Then from equations (9), with $f(\bullet)$ set to f_0 and assuming $\varepsilon^2 \approx 0$, we obtain $x_{AD} = 2\varepsilon$ and $x_{DD} = 1 - 2\varepsilon$ after one generation. Using equations (9) again, the genotype frequencies after two generations are found to be:

$$\begin{aligned} x_{AA} &= 0 \\ x_{AD} &= \varepsilon \\ x_{DD} &= 1 - \varepsilon - \varepsilon \frac{Pv_H}{2Ef_0v_D} \\ x_A &= \frac{Pv_H\varepsilon}{4Ef_0v_D} \\ x_D &= \frac{Pv_H\varepsilon}{4Ef_0v_D} \end{aligned}$$

$$\begin{aligned}
x_H &= 0 \\
x_{AH} &= 0 \\
x_{DH} &= 0
\end{aligned} \tag{10}$$

The frequency of allele A is $x_{AA} + x_A + x_{AD}/2 = P v_H \varepsilon / (4 E f_0 v_D) + \varepsilon/2$. This frequency is less than the initial frequency ε if $P v_H < 2 E f_0 v_D$. This is the condition for the population of DD individuals to be stable to invasion by A mutants and is the same as the condition for $r_D > r_A$ in equations (3).

Similarly, we can show that the condition for a diplontic population to be stable to invasion by allele H is that $r_D > r_H$, and correspondingly for haplontic or haplo-diplontic populations to be evolutionarily stable. Hence the life-cycle strategy that is expected to evolve is the one that maximizes the population growth rate as in equations (3), with $f(\bullet) = f_0$, the equilibrium fertilization probability.

The evolutionary analysis reinforces our conclusions from the population dynamics section that the life-cycle selected is the one that has the highest fitness in terms of propagule production and propagule survival to adulthood. Hence haplonty is evolutionarily stable when the values of p_H or v_H are high, diplonty when those of p_D or v_D are high, and haplo-diplonty when P is large or f_0 small. Since the propagules produced every other generation in a haplo-diplontic population are spores that do not need to be fertilized, haplo-diplonty is selected if the sporophytic fecundity for spore production is much higher than the gametophytic fecundity for egg production, or if the equilibrium fertilization probability of the eggs is low. Hence haplo-diplonty can be selected as a strategy to avoid the risk of non-fertilization of eggs every other generation. When the constant fertilization probability f_0 is less than 1, the presence of the intermediate generation where the propagules do not need to be fertilized increases the proportion of gametes with allele A in the gamete pool. We call this effect gamete amplification of gametes with allele A , resulting in the selection for haplo-diplonty.

In the next section, we use simulations to examine the dynamical convergence to the evolutionarily stable equilibria, and to demonstrate the assumption made in this section that the dynamics of genotype frequency and population size changes result in an equilibrium fertilization probability that has the same value in all the three life-cycles. These simulations also let us consider the effect of gamete amplification on the evolution of the life-cycles in further detail.

Convergence to evolutionarily stable equilibrium

To consider the dynamics of convergence to the evolutionarily stable equilibria, we consider different values of the parameters E , S , P , v_D , v_H , p_H , and p_D and simulate the genotype frequency changes starting with a population consisting of equal proportions of each of the eight genotypes. We model the fertilization function $f(\bullet)$ as a saturating function of the total number of sperm in the gamete pool (S_T), using the Michelis-Menton equation: $f(S_T) = k S_T / (k S_T + 1)$. The total number of sperm in the pool in turn depends on the population size, N . The initial population size is a parameter of the simulations, and population growth between generations is given by the equation $N' = N w$, where w as in equation (9) is the mean fitness of each individual in the population. We consider two cases for the population growth – one is when the population cannot grow beyond a maximum

size N_{max} (corresponding to the carrying capacity), and the second when the population size is not limited.

Table 1 lists three examples of parameter values for which each of the growth rates r_A , r_H and r_D is greater than the other two. In all cases, the evolutionary dynamics results in the fixation of the allele corresponding to the life-cycle with the maximum growth rate – both when the population size is limited as well as unlimited. Furthermore, in the example in Table 1, as in all others attempted by the authors where the parameter values select for haplo-diplonty and the population size is bounded, the haplo-diplontic population eventually consists of either the gametophytic or the sporophytic phase in each generation. Hence the fertilization probability eventually attained by the haplo-diplontic population is the same as that for the haplontic or the diplontic populations.

The above calculations also show that a bounded population always has an equilibrium fertilization probability less than 1, even if it is a value very close to 1. Hence when the survival probabilities of all propagules are equal ($v_H = v_D$), and the average number of eggs produced per individual is equal to the per capita number of spores produced ($E/2 = P$ for a dioecious population and $p_H = p_D = 1$), gamete amplification always selects for haplo-diplonty in a population whose size is limited, and the haplo-diplontic population eventually consists at each generation of only sporophytes or only gametophytes. Since every natural population is limited in size, we conclude that gamete amplification is a general force favouring haplo-diplonty in any broadcast spawning species where the fertilization probability is an increasing function of the total number of sperm in the gamete pool.

Gamete amplification also leads to an initial increase in the proportions of haplo-diplontic genotypes (x_A and x_{AA}) even when the life-cycle eventually favoured is haplonty or diplonty. This results in a faster population growth rate, and quicker attainment of the equilibrium fertilization probability than if these alleles were absent from the population. It is possible that in ephemeral habitats where populations do not persist long enough to allow the evolutionary dynamics to reach its equilibrium, that this transitory advantage of haplo-diplonts suffices to retain allele A in the meta-population. Hence we predict haplo-diplonty to be prevalent among r -selected species, such as invasive algae.

We conclude from simulating the evolutionary dynamics that the fertilization probabilities do attain an equilibrium value when the environment is constant, and the allele that goes to fixation is the one that has the highest growth rate at this fertilization probability. Furthermore, gamete amplification plays an important role in selecting for haplo-diplonty in bounded populations.

DISCUSSION

We conclude from the model that the life-cycle selected is the one with the highest growth rate in terms of propagule production and survival probabilities. In particular, haplo-diplonty may be selected as a means to overcome sperm limitation by avoiding the likelihood of no fertilization at the spore-producing generation. This results in a greater representation of the haplo-diplontic gametes in the gamete pool – an effect we term gamete amplification that selects for haplo-diplonty among populations with limited fertilization probabilities. This also results in a rapid increase in population size and fertilization probability and may make haplo-diplonts better colonizers in ephemeral habitats, leading us to predict haplo-diplonty to be more common among invasive algae. The hypothesis that

Table 1. Simulations of evolutionary dynamics when haplonty, diplonty, and haplo-diplonty are favoured

	Haplonty favoured	Diplonty favoured	Haplo-diplonty favoured
	$P = 4, p_H = 2,$ $v_D = 0.5, v_H = 0.5$	$P = 4, p_H = 1,$ $v_D = 0.6, v_H = 0.5$	$P = 14, p_H = 2,$ $v_D = 0.6, v_H = 0.5$
Population unlimited	$(r_A = r_D = 1, r_H = 4)$ $x_H = 0.999$ in 30 iterations	$(r_A = 1.2, r_D = 1.44, r_H = 1)$ $x_{DD} = 0.98$ in 90 iterations	$(r_A = 4.2, r_D = 1.44, r_H = 4)$ $x_A = 0.6304, x_{AA} = 0.3694$ in 1000 iterations
Population limited to $N_{max} = 1000$	$(r_A = 0.98, r_D = 0.96, r_H = 3.84)$ $x_H = 1$ in 100 iterations	$(r_A = 1.17, r_D = 1.38, r_H = 0.96)$ $x_{DD} = 0.979$ in 100 iterations	$(r_A = 4.12, r_D = 1.38,$ $r_H = 3.84), x_A = 1, x_{AA} = 1$ every alternate generation, by 1000 iterations

Note: For all runs, $E = 8$, $S = 10$, $p_D = 1$, initial population size = 100 and $f(S_T) = kS_T/(kS_T + 1)$, where $k = 0.01$.

alternation of generations may be a strategy to overcome sperm limitation is supported by the prevalence of sperm limitation in the broadcast spawning algae, and the presence of numerous other adaptations in these species to increase sperm concentration. These adaptations include synchronous spawning and optimization of the timing of gamete release (Brawley and Johnson, 1992; Pearson and Brawley, 1996), changes in the plant architecture and the use of pheromones to facilitate gamete contact (Brawley and Johnson, 1992). Furthermore, the gametophytic individuals of heteromorphic species are often better designed to release gametes to ensure gametic encounters (by releasing the gametes in low-velocity environments, for instance), while the sporophytic individuals facilitate spore dispersal (by releasing spores into high-velocity environments) (Bell, 1997; Mable and Otto, 1998).

On the other hand, when haplo-diplonts do not produce propagules at as high a rate, haplonty or diplonty is selected. If the survival probabilities of all propagules were equal and independent of their ploidy, haplontic populations would always grow at a greater rate than diplontic populations since each haplontic zygote divides into multiple haploid spores, while the diplontic zygotes of green and brown algae do not [$p_D = 1$ $p_H = 4$ in most species (Fritsch, 1945)]. In contrast, the observed prevalence of diplonty suggests that the ploidy differences between propagules do result in significant differences in their survival probabilities.

Among algae, the survival probability of propagules includes both the probability of spore or zygote settlement and germination on the sediment, and the probability of the germinated propagule surviving to adulthood. There is no evidence yet that the first process is affected much by the ploidy of the propagule. However, ploidy is likely to play a role in determining the plant's viability. As mentioned in the Introduction, diploids have been hypothesized to have a higher survival probability due to the masking of deleterious mutations or the higher likelihood of the appearance of beneficial mutations. In addition, we suggest that diploidy may also lead to higher viability as a direct consequence of greater genetic variation in the diploid genome. The increased fitness may result from over-dominance at a single locus, or from epistatic interactions between loci.

Diploidy may also confer increased survival probabilities over variable environments, as Mitton and Grant (1984) illustrate with a simple model considering the effect of variation at a single locus over two consecutive environments. Suppose genotype AA has a survival probability of 1 in environment 1 and one of 0.4 in environment 2, and genotype aa the opposite (survival probability 0.4 in environment 1 and 1 in environment 2). If the heterozygote Aa has an intermediate survival probability of 0.7 in both environments, the likelihood of an individual being alive after two seasons (environment 1 followed by environment 2) is 0.4 if its genotype is AA or aa , but 0.49 if it is Aa . Hence genetic variation at a single locus or multiple loci can lead to increased fitness over variable environments. Mable and Otto (1998) suggest in their review of the theories for haplo-diplonty that the time is ripe for models to incorporate environmental changes over space and time. The selective advantage for diploidy that we propose here inherently assumes an environment that changes over time.

The wider range of accommodative responses of a diploid organism to unfavourable environments was suggested by Raper and Flexer (1970) as a reason for selection for an extended diploid phase. This idea has not been previously incorporated into a theoretical framework for the evolution of haplo-diplonty. Goldstein (1992) analysed a two-locus model to examine if a modifier allele increasing the length of the diploid phase would be selected as a result of heterozygote advantage at a linked locus. He deduced that the modifier allele

could increase in frequency whenever a polymorphic equilibrium already exists at the linked locus. Since the likelihood of a polymorphic equilibrium at the linked locus decreases with an increase in the length of the haploid phase, Goldstein concluded that heterozygote advantage at the linked locus is insufficient to explain transitions from haplonty to diplonty. However, any of the large number of loci linked to the modifier allele could contribute either singly or in combination to the heterozygote advantage effect leading to selection for a polymorphic equilibrium. Hence we conclude that this mechanism for the selection for diploidy remains viable.

Empirical support for the hypothesis that the diploid phase may be selected due to its higher genetic variation stems from studies of heterosis that show that individuals with greater within-locus and between-locus variation have increased fitness (Hansson and Westerberg, 2002; Reed and Frankham, 2003; Hughes *et al.*, 2008), as well as studies that demonstrate higher fitness of polyploid individuals compared with diploids (Levin, 1983; Otto and Whitton, 2000; Soltis and Soltis, 2000; Lippman and Zamir, 2007). That the diploid phase is not the dominant one in all haplo-diplontic species, and that diploidy is not the norm in all long-lived algae, indicates that more forces than just the survival advantage of diploids may be involved in the selection for the different life-cycles. We suggest that the effect of alternation of generations on fertilization probability may be one such selective force, favouring haplo-diplonty in low-fertilization probability environments.

Hence this paper shows how the life-history parameters determining the number of propagules produced (E , f , P , p_D , and p_H) and the survival probability of the propagules (v_D and v_H) contribute to the selection for haplonty, diplonty or haplo-diplonty. Previous models for the evolution of ploidy-cycles have focused on the longer-term effects of ploidy, such as weeding out deleterious mutations or increasing the rate of adaptation (e.g. Otto and Goldstein, 1992; Orr and Otto, 1994). In contrast, differences between propagule production and survival rates fundamentally distinguish between the life-cycles, and do so even on shorter time-scales. Moreover, the parameters corresponding to propagule production, fertilization, and survival can be easily measured empirically, and hence the model can be readily tested.

The most direct test of the model would be if individuals of a certain ploidy-cycle could be mutated to viably follow a different ploidy-cycle. The model would be validated if the mutants had a lower growth rate than non-mutants; however, this may be hard to distinguish from the deleterious effects of such a drastic mutation. A second route to testing the model is using comparative studies of closely related species with different ploidy-cycles. Consider three species, each following the haplontic, diplontic, and haplo-diplontic cycles and growing in three different environments. If the species are related closely enough, we can suppose that a viable mutation to a different ploidy-cycle would result in propagule production and survival rates equal to those of the related species following the different ploidy-cycle. To make the comparison even more accurate, transplantations may be carried out to account for the effects of the environment on propagule production and survival probabilities. The model would predict that the resident ploidy-cycle has a higher growth rate than the introduced ploidy-cycle, for each environment. This approach could also be used to test the model prediction that haplo-diplonty is selected due to gamete amplification in environments with limited fertilization probabilities and in ephemeral habitats.

Previous models for the evolution of ploidy-cycles have rarely been tested with the algal groups, due to the lack of data relevant to measuring the long-term effects of ploidy on fitness. On the other hand, much work documents the demography of sea weeds in the field (Thornber, 2006; De Wreede and Klinger, 1988). Many of these studies have focused on the ratio of

gametophytic to sporophytic individuals in a population, and the dependence of this ratio on the fertilization probability (Thornber and Gaines, 2004; Fierst *et al.*, 2005). The data collected from these population studies suffice to test our model.

The different algal taxa exhibit different distributions of the three life-cycles. The basal green algal clades are haplontic, and species of Ulvophyceae, Siphonocladales, and Cladophorales are haplo-diplontic with isomorphic or heteromorphic generations (Pickett-Heaps, 1975; Bold, 1985; Lee, 1999). Hence the transition to haplo-diplonty in green algae involved the increase in length of the zygotic phase before spore formation. We suggest that this transition could have occurred due to the fitness advantage of the zygotic phase as a result of increased genetic variation, or because the resulting sporophyte produces more spores than the parent haploid whose gametes need to be fertilized. Diplonty is rare among the green algae, but much more common in brown algae. The basal brown algal clades are haplo-diplontic and isomorphic. Multiple transitions to haplonty, diplonty, and haplo-diplonty with heteromorphic generations occurred among the derived brown algal taxa (Bold, 1985; Bell, 1997; Lee, 1999). Many red algal species have a three-phase life-cycle with two diploid generations alternating with one haploid generation. Searles (1980) relates this life-cycle to the presence of non-flagellated sperm, and hence the rarity of zygote formation. He suggests that the carposporophytic phase is a mechanism to amplify the propagule production from a single zygote. In our model, this corresponds to a high value of p_D , as contrasted with $p_D = 1$ for green and brown algal species. Hence the three-phase life-cycle of red algae may also be an adaptation to sperm limitation, and a trait whose stability is predicted by this model.

Among all eukaryotic taxa, haplonty may be most primitive and diplonty prevalent among the most derived taxa (Bell, 1994). However, transitions between haplonty, diplonty, and haplo-diplonty have occurred multiple times in the phylogenetic tree, and in different directions. Apart from predicting diplonty in long-lived species, or species in variable environments, and haplo-diplonty in limited or transient populations, or in low-fertilization probability environments, our model does not make specific predictions about the direction of ploidy phase transitions. Instead, it provides a framework for which data from species with different ploidy strategies can be compared to illuminate the drivers behind particular transitions.

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