



The evolutionary advantage of haploid versus diploid microbes in nutrient-poor environments



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HIGHLIGHTS

- We studied the relative advantages of haploidy versus diploidy in microbes.
- We examined the nutrient-limitation hypothesis theoretically.
- Energy conversion efficiency and scaling of mortality with cell size are key.
- We compared our theoretical predictions with empirical observations.

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ABSTRACT

Sexual eukaryotic organisms are characterized by haploid and diploid nuclear phases. In many organisms, growth and development occur in both haploid and diploid phases, and the relative length of these phases exhibits considerable diversity. A number of hypotheses have been put forward to explain the maintenance of this diversity of life cycles and the advantage of being haploid versus that of being diploid. The nutrient-limitation hypothesis postulates that haploid cells, because they are small and thus have a higher surface area to volume ratio, are advantageous in nutrient-poor environments. In this paper, we examine this hypothesis theoretically and determine the conditions under which it holds. On the basis of our analysis, we make the following predictions. First, the relative advantages of different ploidy levels strongly depend on the ploidy-dependent energy conversion efficiency and the scaling of mortality with cell size. Specifically, haploids enjoy a higher intrinsic population growth rate than diploids do under nutrient-poor conditions, but under nutrient-rich conditions the intrinsic population growth rate of diploids is higher, provided that the energy conversion efficiency of diploids is higher than that of haploids and the scaling of mortality with cell size is weak. Second, differences in nutrient concentration in the inflowing medium have almost no effect on the relative advantage of ploidy levels at population equilibrium. Our study illustrates the importance of explicit modeling of microbial life history and population dynamics to understand the evolution of ploidy levels.

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1. Introduction

Sexual eukaryotic organisms are characterized by haploid and diploid nuclear phases (Mable and Otto, 1998). The diploid phase is dominant among most advanced taxa with complex body structures, and many hypotheses have been advanced to explain the evolution of a prolonged diploid phase (Coelho et al., 2007; Crow and Kimura, 1965; Kondrashov and Crow, 1991; Lewis and Wolpert, 1979; Perrot et al., 1991). However, hypotheses that predict that

only diploidy has an adaptive benefit do not satisfactorily explain the evolutionary persistence of haploidy and haploid–diploid life cycles (Hughes and Otto, 1999; Mable and Otto, 1998).

In many organisms, growth and development occur in both haploid and diploid phases, and the relative length of these phases displays considerable diversity (Bell, 1994; Mable and Otto, 1998). For example, eukaryotic algae show various patterns of alternating generations. Especially notable is the diversity of heteromorphic life cycles, in which distinct haploid and diploid generations alternate (Abbott and Hollenberg, 1993; Bell, 1997; Bessho and Iwasa, 2010; Dring, 1992; Van den Hoek et al., 1995). In some species with a heteromorphic life cycle (e.g., family *Laminariaceae*, *Palmaria palmata*, *Kornmannia leptoderma*), the diploid phase develops into large-sized multicellular algal body but the haploid

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phase is microscopic, whereas in others (e.g., genus *Scytosiphon*, family *Bangiaceae*, genus *Monostroma*) the opposite is true (Bell, 1994; Dring, 1992; Hori, 1994).

These life cycle differences are observed in all three major divisions of macroalgae (Chlorophyta, Phaeophyta, and Rhodophyta) across many different lineages (Bell, 1994; Dring, 1992; Hori, 1994), which indicates that the relative dominance of the ploidal phases in algal life cycles is evolutionarily labile. Thus, theoretical studies have focused mainly on the evolutionary mechanisms by which these diverse life cycles are maintained and the trade-offs between being haploid versus being diploid (Coelho et al., 2007; Jenkins, 1993; Lewis, 1985; Nuismer and Otto, 2004; Orr and Otto, 1994; Otto and Marks, 1996).

Various developmental, genetic, and ecophysiological hypotheses have been put forward to explain the maintenance of such diverse life cycles. Developmental hypotheses posit that the diploid cell is essential for the development of complex structures (Bell, 1994; Perrot, 1994), whereas genetic hypotheses focus on the genetic advantages. For example, diploids can repair DNA damage by using the remaining intact chromosome as a template (Michod and Gayley, 1994), mask recessive deleterious mutations (Gerstein and Otto, 2009; Kondrashov and Crow, 1991; Mable and Otto, 2001; Otto and Goldstein, 1992; Otto and Marks, 1996; Perrot et al., 1991), evolve more rapidly (Lewis and Wolpert, 1979; Orr and Otto, 1994), and harbor a greater diversity of recognition molecules to help prevent infection by parasites (M'Gonigle and Otto, 2011; Nuismer and Otto, 2004).

Ecophysiological hypotheses focus on how ploidy affects an organism's adaptation to its environment (Cavalier-Smith, 1978; Lewis, 1985). A positive correlation between nuclear DNA content and cell volume has been reported in angiosperm plants (Bennett, 1972; Martin, 1966; Price et al., 1973), vertebrate animals (Commoner, 1964; Olmo and Morescalchi, 1978; Pagel and Johnstone, 1992), prokaryotic bacteria (Commoner, 1964), and algae (Holm-Hansen, 1969). This correlation is observed across ploidy levels and regardless of the number of nuclei in a cell or the cell size in angiosperms (Jovtchev et al., 2006; Melaragno et al., 1993), yeast (Galitski et al., 1999), and algae (Goff and Coleman, 1990). A strong correlation between the DNA content and the cell cycle length has also been reported (Bennett, 1971; Van't Hof, 1965; Van't Hof and Sparrow, 1963). These observations led Cavalier-Smith (1978) to suggest that the evolution of ploidy levels is a by-product of selection for cell size: conditions favoring small individuals with rapid growth rates select for haploidy, whereas conditions favoring large individuals select for diploidy. This is known as the Cavalier-Smith hypothesis.

Lewis (1985) has pointed out that the Cavalier-Smith hypothesis is insufficient because it does not explain the successional patterns of unicellular marine algae. Under the classical r- and K-selection hypothesis for a freshwater environment, small algae with higher population growth rates should appear early and large taxa occur toward the end of the succession when nutrients are limited. However the generally acknowledged successional pattern in marine environments is one where unicellular diploid diatoms tend to dominate early in a sequence of succession (Lewis 1985). To overcome the shortcomings of the Cavalier-Smith hypothesis, Lewis proposed a nutrient-sparing hypothesis (or nutrient-scarcity hypothesis), which explains the evolution of haploid organisms in relation to the energy supply. He suggested that haploidy might be more advantageous than diploidy under nutrient-limited conditions because haploid organisms have lower DNA replication costs.

The combination of these two hypotheses is known as the nutrient-limitation hypothesis (or nutrient-saving hypothesis). According to this hypothesis, diploids, which are simply double haploids, grow as fast as, or possibly faster than, haploids in nutrient-rich environments; although having twice as much DNA means that mRNA transcription can occur twice as fast, the speed advantage is canceled out by the larger cell volume. Therefore, the nutrient utilization efficiency of

diploids is almost the same as that of haploids. In contrast, haploid cells enjoy an advantage in nutrient-poor environments, because the smaller haploid cells are better able to deal with nutrient scarcity owing to their greater ratio of surface area to volume (Coelho et al., 2007; Mable and Otto, 1998; Otto and Gerstein, 2008; Perrot, 1994).

The nutrient-limitation hypothesis has been tested by competition experiments performed with unicellular yeasts in chemostats and by measurement of body growth rates in multicellular juvenile red macroalgae raised under different nutrient conditions. The results of these experiments are not conclusive, however. For example, Adams and Hansche (1974) reported no significant difference in the maximum population growth rate between haploid and diploid yeasts in nutrient-rich chemostats, but they also found that haploid cells grew more rapidly than diploid cells when growth was limited by organic phosphate availability. Similarly, Glazunov et al. (1989) reported that diploid yeasts displaced haploid yeasts in rich media, although they also found that haploid cells had an advantage over diploid cells in minimal media, and in the presence of a competitor (the yeast *Pichia pinus*). However, Naidhardt and Glazunov (1991) reported that diploids completely displaced haploids in both rich and minimal media, and diploids also have an advantage over haploids in the presence of a competitor. Similarly in an experiment comparing growth rates between isomorphic haploid and diploid phases in the juvenile red alga *Gracilaria verrucosa*, Destombe et al. (1993) found that the haploid stage had a growth advantage under nutrient-poor conditions and diploids had an advantage in nutrient-rich seawater. In the isomorphic red alga *Polcavernosa debilis*, however, Littler et al. (1987) reported no significant differences in net photosynthesis or calorific content across ploidy levels.

In this paper, we develop life history models of unicellular microbes with ploidy-dependent parameters to help us to understand these experimental outcomes.

2. Model

To determine the effect of nutrients on the relative advantage of haploid versus diploid phases, we developed two models of a unicellular microbe with asexual reproduction. The first model, which is the simplest, assumes that nutrient levels are fixed and populations of microbes grow exponentially. In this density-independent model, we evaluate the relative advantage of the two ploidy levels by comparing their intrinsic population growth rates. In the second model, we incorporate density-dependence in the population dynamics and quantify the relative advantage of the different ploidy levels by determining under what circumstances one outcompetes the other. Parameters and variables in our model are listed in Table 1.

2.1. Life history of unicellular microbes

Both models assume the same microbial life history. The microbes of both ploidy levels proliferate asexually (or vegetatively) by binary fission. A generation starts at the ontogenetic time $\tau=0$ and ends at $\tau=T_p$. Suffix p is ploidy dependent; when $p=h$, the generation is haploid, and when $p=d$, it is diploid.

Within the lifespan of a microbe, the cell volume V_p increases according to the following differential equation and initial condition:

$$\frac{dV_p}{d\tau} = e_p U_p (V_p, N), \quad \text{for } 0 \leq \tau \leq T_p, \quad (1a)$$

$$V_p(0) = v_p, \quad (1b)$$

where U_p denotes the rate of nutrient uptake per individual; N is the nutrient level, and e_p is the energy conversion efficiency into cell structure, which is assumed to be constant.

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