

NUTRIENT SCARCITY AS AN EVOLUTIONARY CAUSE OF HAPLOIDY

WILLIAM M. LEWIS, JR.

Department of Environmental, Population, and Organismic Biology,
University of Colorado, Boulder, Colorado 80309*Submitted February 13, 1984; Accepted September 23, 1984*

Ploidy levels vary among categories of organisms, but existing evolutionary explanations for this variation are incomplete. The largest and most highly differentiated organisms are diploid. Many, but by no means all, of the simplest organisms are haploid, and organisms of intermediate complexity can be haploid, haplo-diploid (showing alternation of haploid and diploid generations), or diploid (Raper and Flexer 1970). The general trend from haploidy to diploidy along the gradient from simple to complex organisms is the foundation for existing general theories that explain ploidy levels. According to these general theories, diploidy offers three kinds of advantages related to organism function or fitness: (1) genetic buffering; (2) more subtle control of development and function; and (3) heterosis (Williams 1966; Raper and Flexer 1970). In addition, Bell (1982) has pointed out, partly following Svedalius (1927), that diploidy offers the possible advantage of increased variety in gamete or zygote phenotypes. If these are indeed categorical advantages to diploidy, then there must be some companion explanation for the persistence of haploidy in numerous groups of simple organisms. Some default explanations might derive from the failure of simple organisms (or the genes for which they are a vehicle [Dawkins 1983]) to benefit from genetic buffering or heterosis, from subtle control over development and function, or from higher genetic diversity in gametes and progeny. These are very difficult propositions to defend, especially since diploidy and haplo-diploidy are found in several important groups of simple, single-celled organisms. If such default explanations are not correct, then there must be some other explanation that will take into account the tendency for simple organisms to be haploid without denying the advantages of diploidy in many categories of organisms, including some single-celled groups. The only attempt at a comprehensive explanation is Cavalier-Smith's hypothesis hinging on *r*- and *K*-selection. Cavalier-Smith's hypothesis is innovative in its recognition of nongenetic factors, and specifically those related to cell size, in accounting for ploidy variations. As will be shown here, however, Cavalier-Smith's hypothesis is not fully consistent with the known distribution of ploidy levels.

The purpose of this paper is to show how haploidy can be advantageous for certain classes of organisms under certain conditions. The proposed advantages of

haploidy are based on nutrition rather than genetics. The essence of the explanation is that haploidy can sometimes confer significant ecological advantages that serve as a powerful counterweight to the genetical advantages of diploidy, thus causing haploidy to be retained. The conditions for retention of haploidy are defined by three sets of factors: (1) the relationship between DNA, cell size, and mitotic cycle time; (2) the qualitative shift in selection pressures influencing cell size when organisms are composed of numerous cells instead of one or a very few cells; and (3) the qualitative differences in selection pressures affecting organisms that obtain nutrients and energy simultaneously, as opposed to those that obtain nutrients and energy by separate processes. The explanation will be tested for concordance with the distribution of ploidy in several phylogenetic lines.

DNA AND CELL SIZE

There is a strong positive relationship between DNA and cell volume in organisms. This has been demonstrated for higher plants (Price et al. 1973), vertebrates (Commoner 1964), eukaryotic algae (Holm-Hansen 1969), and even procaryotes (Commoner 1964). The relationship between DNA and cell size is found not only between species, but also within species for cells of different ploidy. The haploid amount of DNA for an organism is not related to its complexity (Cavalier-Smith 1978*a*); hence, the great variation in haploid DNA among organisms has been referred to as the "C-value paradox" (Thomas 1971).

Cavalier-Smith (1978*a*, 1978*b*), in attempting to resolve the C-value paradox, has proposed that DNA serves both genetic and structural purposes. According to this hypothesis, the sole purpose of the nontranscribed DNA is to determine the size of the nucleus, which in turn determines the size of the cell. The need for this "structural" DNA is explained in terms of the necessity for information flow via RNA between the nucleus and the cytoplasm of the cell, which requires a certain minimum amount of nuclear membrane and, thus, a certain nuclear volume per unit of cytoplasm. This bold hypothesis is consistent with a number of phenomena that are otherwise difficult to explain, including the apparent excesses of DNA that do not perform known genetic functions. The great general weakness of the hypothesis is that DNA is metabolically and ecologically expensive (especially because of its high phosphorus and nitrogen content); Cavalier-Smith's theory implies that, over the entire history of eukaryotes, no cheaper mechanism to control nucleus size has ever arisen. One wonders, for example, why all nuclei are not flattened or branched to improve surface-to-volume ratio and thus to reduce DNA requirement, if the main role of much of the DNA is simply to determine the ratio of nuclear membrane to cytoplasm.

Cavalier-Smith's hypothesis is not the only one that has been proposed to account for the great variation in DNA among cells. Dawkins (1976, 1983) argues that inactive DNA is made up of genes that have been selected for their ability to be carried along with the active DNA, possibly even to the detriment of the organism in which the DNA resides. If so, then the inactive DNA could be regarded as a sort of parasitic load that is carried by extra cytoplasm. This explanation will be especially difficult to apply to taxa that reproduce largely or

TABLE 1
 OVERVIEW OF PLOIDY LEVELS IN ORGANISMS (slightly modified
 from Raper and Flexer 1970)

Taxon	Ploidy
Animals and animallike Protista	
Protozoa	Diploid (a few haplo-diploid, haploid)
Animals	Diploid
Plants and plantlike Protista	
Algae	Haploid, haplo-diploid, diploid
Mosses and liverworts	Haplo-diploid
Ferns	Haplo-diploid
Seed plants	Diploid
Fungi and funguslike Protista	
Myxomycetes	Haplo-diploid
Uniflagellate water molds	Haploid, haplo-diploid (a few diploid)
Biflagellate water molds	Diploid
Zygomycetes	Haploid
Hemiascomycetes	Haploid, haplo-diploid
Euascomycetes	Haplo-dikaryotic
Basidiomycetes	Haplo-dikaryotic

exclusively by asexual means, since the propagation of the gene and the propagation of the organism are even more closely linked in such taxa than in sexual ones. Other authors propose a yet-unspecified genetic mechanistic function for the inactive DNA (reviewed in Dawkins 1983).

For present purposes it is not necessary to know the cause of the relationship between DNA and cell size, if one can accept that there is some kind of essential connection between DNA and cell volume. This assumption seems safe in view of the appearance of the relationship in all major evolutionary lines.

PHYLOGENETIC DISTRIBUTION OF PLOIDY LEVELS

Table 1 provides an overview of the distribution of ploidy levels in large groups of organisms. Haploidy is found in the autotrophic Protista and in the simplest Plantae (Chlorophyta), but not in higher plants. Among the Animalia and heterotrophic protists, haploidy is found only in a few Protozoa. In the Fungi, haploidy is characteristic of a few simple forms, but not of many simple ones nor of any complex ones. Haplo-diploidy (alternation of generations) is common in autotrophs of intermediate complexity, and is found in a few Protozoa (Foraminifera) and some Fungi. The larger and more complex Animalia and Plantae are diploid, as are Protozoa. A functional equivalent to diploidy, haplo-dikaryosis (organism contains haploid nuclei of two types), is found in the advanced Fungi.

For the algae, table 1 is overly general and thus fails to reveal some patterns in the distribution of ploidy levels that are especially useful in evolutionary analysis. Table 2 provides a more complete breakdown for algae in which groups with different ploidy levels are separated. For each group, the dominant ploidy type is

TABLE 2

SUMMARY OF PLOIDY LEVELS, COMPLEXITY, AND GROWTH TYPE IN THE EUKARYOTIC ALGAE
(mainly from Bold and Wynne 1978; Goddard 1966)

	Ploidy	Relative Complexity	Growth Type
Chlorophycophyta			
Volvocales*	Haploid	Low	Suspended
Tetrasporales*	Haploid	Low	Suspended/Attached
Chlorococcales*	Haploid (?)	Low	Suspended/Attached
Chlorosarcinales	Unknown	Low	Suspended/Attached
Chlorellales*	Unknown	Low	Suspended
Ulotricales	Haploid, haplo-diploid	Intermediate	Attached/Suspended
Chaetophorales	Haplo-diploid†	Intermediate	Attached
Oedogonales	Haploid	Intermediate	Attached
Ulvales	Haplo-diploid†	Intermediate	Attached
Cladophorales	Haplo-diploid†	High	Attached
Acrosiphonales	Haplo-diploid	High	Attached
Caulerpales	Haplo-diploid, diploid	High	Attached
Siphonocladales	Diploid	High	Attached
Dasycladales	Haplo-diploid	High	Attached
Zygnematales*	Haploid	Low	Suspended/Attached
Charophyta	Haploid	High	Attached
Euglenophycophyta*	Unknown	Low	Suspended
Phaeophycophyta	Haplo-diploid, diploid	High	Attached
Chrysophycophyta			
Chrysophyceae*	Haploid	Low	Suspended
Prymnesiophyceae	Haplo-diploid	Low	Suspended
Xanthophyceae	Haploid	Low	Suspended/Attached
Eustigmatophyceae	Unknown	Low	Suspended/Attached
Chloromonadophyceae	Unknown	Low	Suspended/Attached
Bacillariophyceae*	Diploid	Low	Suspended/Attached
Pyrrophyphyta*	Haploid	Low	Suspended
Rhodophycophyta	Haplo-diploid	High	Attached
Cryptophycophyta*	Unknown	Low	Suspended
Cyanophyta*	Haploid	Low	Suspended/Attached

* Major contributors to phytoplankton.

† Also some haploids.

indicated. These categories cannot be taken as absolute, since ploidy has been studied very sparingly in many groups of algae. Table 2 also categorizes each taxon as being simple, intermediate, or high in relative complexity by comparison with other algae. Taxa characterized as being simple occur as single cells, small colonies, or coenobia lacking differentiation. Taxa characterized as intermediate show a certain amount of differentiation and consist of colonies (typically filaments) of larger size. The complex forms show differentiation that is advanced among algae and typically are large. Table 2 also provides information on the distribution of suspended and attached forms among these major taxa. As might be expected, the complex and intermediate forms are attached to substrates, with very few exceptions (e.g., *Sargassum*). The smaller, simpler forms frequently grow in suspension, although it is also possible for these to grow on substrates.

EXPLANATIONS FOR THE PHYLOGENETIC DISTRIBUTION OF PLOIDY

The selection pressures affecting individual cells may be very different according to whether the cells are themselves organisms or simply components of a multicellular organism (Cavalier-Smith 1978*a*, 1978*b*). A multicellular organism may be subjected to selection favoring small size, but this does not necessarily dictate that the cells composing the organism need to be small. On the other hand, in organisms consisting of a single cell or a very small number of cells, selection for small size in the organism is in effect selection for small cell size. Thus, any analysis of cell DNA content or cell size must take into account the qualitatively different evolutionary constraints on cells in small, simple organisms in contrast to cells in larger, more complex organisms.

Cavalier-Smith (1978*a*) has proposed that the gradient from haploidy to diploidy that parallels phylogenetic complexity gradients is basically a matter of *r*- and *K*-selection. According to this line of reasoning, small organisms are *r*-selected and, since selection pressures favoring small size are acting directly on the cells, haploidy is favored because it allows smaller inventory of DNA, which in turn implies a faster mitotic cycle time and a higher maximum growth rate. This is an ingenious explanation, but it glosses over the fact that a number of groups of very simple organisms are diploid, and it assumes that simple organisms showing haploidy are all strongly *r*-selected.

Contradictions of the *r*- and *K*-selection hypothesis are easily shown for the planktonic algae, where the ecological information base is good. Successional sequences of algae have been studied extensively (Smayda 1980), especially in freshwater environments (Hutchinson 1967; Lewis 1978; Reynolds 1980). A successional sequence is initiated by disturbance of layering, with associated changes in light and nutrients, in a water column. Subsequent to the disturbance, autogenic forces (i.e., alterations in the environment caused by the organisms themselves) cause sequential replacement of one group of taxa by another. The most strongly *r*-selected taxa should appear early in such a sequence, when the conditions for growth are best, and the *K*-selected taxa should occur toward the end of the sequence, when nutrients are scarce and grazing and parasitism are most pronounced. Although there is a great deal of variability from one lake to another, it is generally acknowledged that the diatoms appear early in the successional sequence, the green algae appear in the middle, and the dinoflagellates and blue-green algae appear toward the end. For marine environments, it also appears that diatoms dominate early in a sequence and dinoflagellates dominate later (Margalef 1978). Thus, the one important group of autotrophic unicellular diploids (the diatoms) appears just when the conditions should, according to the hypothesis of Cavalier-Smith, make their appearance least likely.

Cavalier-Smith's hypothesis can also be questioned on more general grounds. For example, it is not at all clear that algae of intermediate and higher complexity are more likely than the simplest algae to be *K*-selected. Although the organism units are larger because of the more extensive aggregation of cells, the cells of many of the larger algae are so poorly integrated that they are almost independent

physiologically. It is difficult to see how such organisms would necessarily be less strongly selected for rapid growth than unicells.

The *r*- and *K*-selection dichotomy may actually be a handicap rather than a help in analyzing the connection between haploidy and selective forces associated with growth rates; the specific nature of the selective forces is more relevant than the *r* and *K* dichotomy. The degree to which the growth potential of an individual organism is realized can be expressed for the most part in terms of two kinds of factors: energy supply and nutrients. An organism that feeds on living biomass obtains its energy and its nutrients simultaneously. A saprophyte can also obtain energy and nutrients simultaneously, but, if the nonliving organic matter on which it feeds diverges chemically from living organic matter, it may need to supplement its caloric intake by additional and separate nutrient intake. For an autotroph, acquisition of nutrients and of energy are completely dissociated. In fact, the temporal and spatial distributions of these two categories of resources are often negatively correlated. These basic nutritional distinctions between groups of organisms are important in the explanation of ploidy distributions.

Since the interception of light and the uptake of nutrients are only linked indirectly in autotrophs, it will often happen that the growth of an organism will be suppressed by lack of one when the other is present in quantity. For suspended algae, the critical nutrients are most often the macronutrients phosphorus and nitrogen (Round 1981). Since the boundary between limitation by one nutrient and another appears to be quite sharp (Rhee 1978), failure of healthy algal cells to grow in the presence of adequate sunlight is typically evidence of either phosphorus or nitrogen limitation (sometimes silicon limitation for diatoms or occasionally a micronutrient). Nutrient scarcity is the rule rather than the exception during the growing season in lakes and oceans (Parsons et al. 1977; Wetzel 1983). Not only does nutrient availability appear to govern the productivity and temporal pattern of abundance for suspended algae in fresh waters and in oceans, but nutrient depletion is considered to be among the most important explanations for the sequential replacement of one algal taxon by another during the growing season. From this perspective, it is clear that most unicellular algal taxa have been subjected to very strong selection pressures favoring efficient uptake, storage, and utilization of phosphorus and nitrogen.

Reduction of the DNA inventory is a powerful nutrient-sparing mechanism, and haploidy is an obvious means by which DNA content can be held to a minimum for an organism with a given genome design. There is a direct saving of phosphorus and nitrogen that is accounted for by the investment of these elements in DNA. For example, in a cell that does not have extensive inactive phosphorus stores, about 10% of the phosphorus is accounted for by DNA (Rhee 1973). Thus, a haploid has half the investment in DNA phosphorus of a diploid, and this would amount to about 5% of the total phosphorus inventory for a fixed cell size. More importantly, however, the necessary connection between DNA content and cell size dictates that all other phosphorus inventories in the cell will be approximately doubled if the haploid becomes a diploid. Thus, the nutrient-sparing effect of haploidy saves approximately 25%–50% of any nutrient because a haploid cell is

50%–75% as big as its diploid counterpart. Under circumstances in which nutrient limitation is continually determining the ability of organisms to reproduce, selection pressure favoring nutrient-sparing can be obviously very important, even in the face of some direct genetic disadvantages to haploidy by comparison with diploidy. In the unicellular algae, the organism and the cell are identical. Selection pressures favoring small organism size will therefore favor small cell size. Furthermore, because they are frequently suspended, unicellular algae are subjected to especially rigorous selection for nutrient-sparing mechanisms. Attached algae typically have access to larger supplies of critical nutrients because virtually all submerged substrates concentrate and regenerate nutrients. Thus substrate-living taxa more frequently compete for space or light than do suspended algae, although the distinction is not absolute. Haploidy is the rule in unicellular algae that live in suspension because these organisms experience the greatest selection pressures for nutrient-sparing.

The diatoms are exceptional among the simplest algae in their retention of diploidy, despite the fact that they are important contributors to the suspended algae in both freshwater and marine environments. This exception, however, is consistent with the nutrient-sparing hypothesis because of the position of the diatoms early in the successional sequence when nutrients are most abundant. Thus, from the viewpoint of phytoplankton succession patterns, diploidy makes much more sense in the diatoms than in any other group.

In the larger and more complex algae, retention of haploidy is of diminished importance for two reasons. First, the frequency and intensity of nutrient limitation are almost certainly less because of substrate contact in these organisms. Second, selection pressures related to size are focused on individuals, and the linkage between individuals and cells becomes more and more diffuse as organisms become larger. Thus, a large alga may be subject to certain selection pressures related to size, but these selection pressures are insensitive to the difference between an organism composed of 10,000 haploid cells as opposed to 5,000 diploid ones. Under these conditions, the advantages of diploidy (presumably genetic advantages) become manifest because they are not opposed effectively by selection pressures associated with organism size. This explains why the attached algae of intermediate or high complexity are not haploid. The one exception is the Charophyta. A single exception does not invalidate the hypothesis, however, since haploidy may be advantageous in a large attached form if the number of cells is of direct selective importance (for reasons yet unknown), and if nutrient limitation is a consistent selective factor for the group. It is interesting in this connection that the charophytes specialize in oligotrophic environments where nutrients are scarcest (Hutchinson 1975). Furthermore, all charophytes that have been studied cytologically appear to be anciently polyploid; each individual has at least two sets of chromosomes. Thus, while their life-cycle pattern is such that the dominant portion is gametophytic, multiple chromosome sets are present in the gametophytes. Grant and Proctor (1972, 1980) have argued that polyploidy in this group has, in effect, provided a genetic substitute for diploidy.

Most of the algae that are not haploid are haplo-diploid rather than diploid. As a rule, the haploid phase of the life cycle involves a very small organism, often with

a suspended phase. The selection pressures operating on this phase of the life cycle are more like those affecting simpler algae. The diploid phase of the life cycle is typically larger, and thus experiences selection pressures associated with large, complex attached forms.

Although the nutrient-sparing hypothesis for haploidy is consistent with the known distribution of haploidy, haplo-diploidy, and diploidy in the algae, it must also be consistent with ploidy distribution in a broader selection of taxa in order to be considered a viable general explanation of ploidy. The Protozoa are single cells, but are not subject to selection pressure for haploidy because they obtain macronutrients and energy simultaneously, and the rate at which they obtain these is a function of size. Thus, there is no nutritionally based categorical selection pressure against large size in these organisms, and this explains why the Protozoa are diploid. A few taxa of Protozoa are haploid, but these may well feed on sufficient amounts of nonliving particulate matter that the uptake of macronutrients is a matter of selective importance to them. In multicellular animals, the cells are diploid, as expected from the nutrient-sparing hypothesis. Not only do these organisms obtain their macronutrients and their energy at the same time, but they also consist of large enough numbers of cells that the selection pressures favoring large or small organisms need not affect individual cell sizes.

The mixture of ploidy levels found in the simple Fungi is consistent with the nutrient-sparing hypothesis. The nutrient-sparing pressures on unicellular saprophytes will vary greatly according to the food type, which dictates the need for supplementary nutrients. Sources that are depleted in macronutrients will require the organism to rely on direct uptake of macronutrients for growth. If these macronutrients are scarce, haploidy will be favored. In view of the very poor background of basic ecological information on Fungi, however, it is not possible to go beyond this and examine the specific nutrient environments of Fungi to determine their concordance with the nutrient-sparing hypothesis. In the higher Fungi, the predicted shift to emphasis on diploidy (dikaryotic condition) occurs as the organism becomes large enough that selection pressures influencing size are irrelevant to ploidy.

The nutrient-sparing hypothesis is consistent with the observed distribution of ploidy levels among organisms, and provides a sufficiently powerful selective force to oppose the beneficial effects of diploidy in organisms for which body-size selection directly affects cell size.

SUMMARY

Diploidy is characteristic of complex organisms, although it also appears in numerous groups of simple organisms. Many groups of simple organisms are haploid or haplo-diploid. Diploidy is widely considered to have certain categorical advantages that account for its appearance in the more complex members of all evolutionary lines. Any categorical advantage of diploidy begs an explanation of the widespread retention of haploidy among simple organisms, however. The retention of haploidy can be explained on a nutritional basis. There is an essential connection of unknown cause between the amount of DNA and cell size; more

DNA maintains more cytoplasm. Factors favoring small size will thus favor haploidy (minimal DNA) in a single-celled organism. Multicellular organisms are not similarly affected because they can reduce the number of cells, rather than reducing cell size in response to size-reducing selection pressure. The most general of size-reducing selection pressures is nutrient scarcity. For unicellular organisms, this selection pressure is probably most pronounced in taxa that obtain their energy and their nutrients by processes subject to temporal separation (autotrophs) and that live in environments where nutrients are frequently exhausted (plankton environments). In contrast, unicells that obtain energy and nutrients simultaneously (e.g., Protozoa) are not subject to the same selection pressures and are expected, therefore, to be diploid, as they are. The nutrient-sparing hypothesis is generally consistent with the sporadic distribution of haploidy among unicellular organisms, and thus appears to explain why haploidy is retained in some groups and not others.

ACKNOWLEDGMENTS

This work was supported by a fellowship from the John Simon Guggenheim Memorial Foundation and by NSF Grant 80-03883. I am grateful to J. B. Mitton, M. C. Grant, G. Bell, and two anonymous reviewers for helpful comments.

LITERATURE CITED

- Bell, G. 1982. *The masterpiece of nature*. University of California Press, Berkeley.
- Bold, H. C., and M. C. Wynne. 1978. *Introduction to the algae*. Prentice-Hall, Englewood Cliffs, N.J.
- Cavalier-Smith, T. 1978*a*. Nuclear volume control by nucleoskeletal DNA, selection for cell volume and cell growth rate, and the solution of the DNA C-value paradox. *J. Cell Sci.* 34:247-278.
- . 1978*b*. *r*- and *K*-tactics in the evolution of protist developmental systems: cell and genome size, phenotype diversifying selection, and cell cycle patterns. *Biosystems* 12:43-59.
- Commoner, B. 1964. Roles of deoxyribonucleic acid in inheritance. *Nature (Lond.)* 202:960-968.
- Dawkins, R. 1976. *The selfish gene*. Oxford University Press, Oxford.
- . 1983. *The extended phenotype*. Freeman, Oxford.
- Godward, M. B. E. 1966. *The chromosomes of the algae*. St. Martin's, New York.
- Grant, M. C., and V. W. Proctor. 1972. *Chara vulgaris* and *C. contraria*: patterns of reproductive isolation between two cosmopolitan species complexes. *Evolution* 26:267-281.
- . 1980. Electrophoretic analysis of genetic variation in the Charophyta I: Gene duplication via polyploidy. *J. Phycol.* 16:109-115.
- Holm-Hansen, O. 1969. Algae: amounts of DNA and organic carbon in single cells. *Science* 163:87-88.
- Hutchinson, G. E. 1967. *A treatise on limnology*. Vol. II: Introduction to lake biology and the limnoplankton. Wiley, New York.
- . 1975. *A treatise on limnology*. Vol. III: Limnological botany. Wiley, New York.
- Lewis, W. M., Jr. 1978. Dynamics and succession of the phytoplankton in a tropical lake. *J. Ecol.* 66:849-880.
- Margalef, R. 1978. Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta* 1:493-509.
- Parsons, T. R., M. Takahashi, and B. Hargrave. 1977. *Biological oceanographic processes*. 2d ed. Pergamon, New York.
- Price, H. J., A. H. Sparrow, and A. F. Nauman. 1973. Correlations between nuclear volume, cell volume and DNA content in meristematic cells of herbaceous angiosperms. *Experientia* 29:1028-1029.

- Raper, J. R., and A. S. Flexer. 1970. The road to diploidy with emphasis on a detour. *Symp. Soc. Gen. Microbiol.* 20:401-432.
- Reynolds, C. S. 1980. Phytoplankton assemblages and their periodicity in stratifying lake systems. *Holarct. Ecol.* 3:141-159.
- Rhee, G. Y. 1973. A continuous culture study of phosphate uptake, growth rate, and polyphosphate in *Scenedesmus* sp. *J. Phycol.* 9:495-506.
- . 1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnol. Oceanogr.* 23:10-25.
- Round, F. E. 1981. *The ecology of algae.* Cambridge University Press, Cambridge.
- Smayda, T. 1980. Phytoplankton species succession. Pages 493-570 in I. Morris, ed. *The physiological ecology of phytoplankton.* University of California Press, Berkeley.
- Svedalius, N. 1927. Alternation of generations in relation to reduction division. *Bot. Gaz.* 83:362-384.
- Thomas, C. A. 1971. The genetic organization of chromosomes. *Annu. Rev. Genet.* 5:237-256.
- Wetzel, R. G. 1983. *Limnology.* 2d ed. Saunders, New York.
- Williams, G. C. 1966. *Adaptation and natural selection.* Princeton University Press, Princeton, N.J.