

PHYTOPLANKTON COMMUNITY ECOLOGY: The Role of Limiting Nutrients

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INTRODUCTION

This paper is a summary and synthesis of the role of nutrients and spatial and temporal fluctuations in controlling the species composition, diversity, and seasonal succession of planktonic algal communities. We do not review the full breadth and depth of the literature that has appeared since the seminal papers by Hutchinson (34) and Dugdale (19). Rather, we focus on some of the major questions and hypotheses, and evaluate these in light of their consistency with observation and experimentation. Because the combined net effect of limiting nutrients, major ions, pH, and other physical factors ultimately determines the reproductive rate of a local algal population, we first briefly review the data on the role of these factors in phytoplankton ecology. We then review the theory of resource competition and apply it to the questions of equilibrium versus nonequilibrium approaches, seasonal succession, and multitrophic level effects in phytoplankton com-

munities. We suggest that a mechanistic, resource-based approach can be expanded to include many important aspects of the physical and biotic habitat.

Since the earliest days of phytoplankton ecology, nutrients have been invoked as one of the variables controlling phytoplankton community structure and biomass (35, 123). The relationship between phosphorus concentration and chlorophyll (17) suggests, and numerous bioassay experiments have repeatedly demonstrated, that phosphorus, and at times nitrogen and silicon, are limiting resources. Whole-lake enrichment experiments (97, 98, 99) demonstrated clearly that phosphorus additions increase algal biomass and that the proportions of the added nutrients (such as N:P ratios) have a dramatic effect on the algal species composition. A reverse 'experiment' was performed on Lake Washington (20) when diversion of sewage resulted in decreased loadings of phosphorus relative to nitrogen, with concomitant decreases in phytoplankton biomass and changes in species composition (cf Figure 2D; V. H. Smith, personal communication). In addition to phosphorus and nitrogen, silicon (39), CO₂ (109), and light (120, 126) have been suggested to have selective effects on phytoplankton species. Other resources such as iron and trace metals may be limiting in certain situations (32).

As reviewed below, there has been considerable experimental documentation of the importance of nutrient limitation in determining the algal species composition of lakes. Such experimental work contrasts with the more traditional, observational approach that has characterized phytoplankton ecology since the turn of the century. Correlation analyses have been the primary methodology employed, usually based on field observations of species composition and water chemistry (60, 78). Laboratory studies designed specifically to test the validity of the conclusions derived from correlation analyses are few, but they have shown that correlation and causation are rarely the same (48, 49, 70, 108). Even though experimental investigations have indicated that much of the "phycological dogma" (10) collectively known as phytoplankton ecology is open to question, it seems that many systematic phycologists are unwilling to question their primary methodological approach. This is unfortunate because the literature on phytoplankton ecology is used by environmental scientists to make management decisions and by paleoecologists who use fossil remains of algae (e.g. diatom frustules) as indicators of ancient environments (9, 74, 92).

The correlation between chloride ion concentration and phytoplankton community composition [the "halobien system" (45, 46, 77, 78, 81)] has been widely used by diatom ecologists (12, 60, 100), though the importance of Cl⁻, per se, has been repeatedly questioned (e.g. 13, 14). Similarly, the suggestion of the possible importance of Na⁺ rather than Cl⁻ (77, 78) is based on primitive data (94). The few experimental studies performed on

algae suggest that major anions (Cl^- , SO_4^{2-} , HCO_3^-) and osmotic pressure can affect algal growth rates (108) and that cation concentrations affect the kinetics of phosphate uptake (27, 95). Many more such studies will be needed to determine whether there is a mechanistic, causative basis for the observed correlations between cation and anion concentrations and algal community structure.

Strong correlations between the species composition of algal communities and the inorganic carbon system (i.e. pH, pCO_2 , alkalinity, dissolved inorganic carbon, etc) have also repeatedly been observed (10, 60, 61, 70–73, 77, 78, 109). The best-studied correlation involving the inorganic carbon system is between the structure of diatom communities and pH (33), which forms the basis of Nygaard's indexes (16, 67, 75). These indexes can be used to compute the functional pH of a body of water from the species composition of the diatom flora. However, the underlying physiological and mechanistic basis for the correlation is not known and has not been investigated (but see 50, 71, 72, 73, 109, 125). Because pH is the master variable in the chemistry of aquatic systems (107) it must affect the kinetics of nutrient uptake and control the chemical species of most of the nutrient ions algae require. Some work has been done on the forms of carbon taken up by algae (50), but little is known about the ability of algae to take up particular chemical species of metals, silicon, or even phosphorus.

THEORY

Given that resources do limit the growth of phytoplankton, it is possible to construct various models of phytoplankton-resource interactions (e.g. 19, 54, 111, 113, 114) that embody some degree of "physiological reality" and state explicitly that the mechanism of interaction between species is competition for limiting resources. We introduce the theory with a simple model. The resources we consider—light, nitrogen, phosphorus, silica—are essential resources (112, 114), and algae use them in a threshold manner (18, 89). The models can easily be adapted to include interacting resources (112, 114).

One simple model describing the relationship between the growth rate of an algal species and the availability of a limiting resource is the Monod model [(2, 7, 40, 42, 68, 101, 114, 115); Figure 1A, B]. The two parameters of this model summarize the ultimate effect of uptake and utilization on reproductive rate (11, 18, 41, 111, 115). The Monod model can be used to develop a graphical-mechanistic model of competition for two potentially limiting essential resources (1, 55, 63, 82, 110, 112, 114). We use these graphical models throughout this paper. See references 112 and 114 for an explicit mathematical treatment.

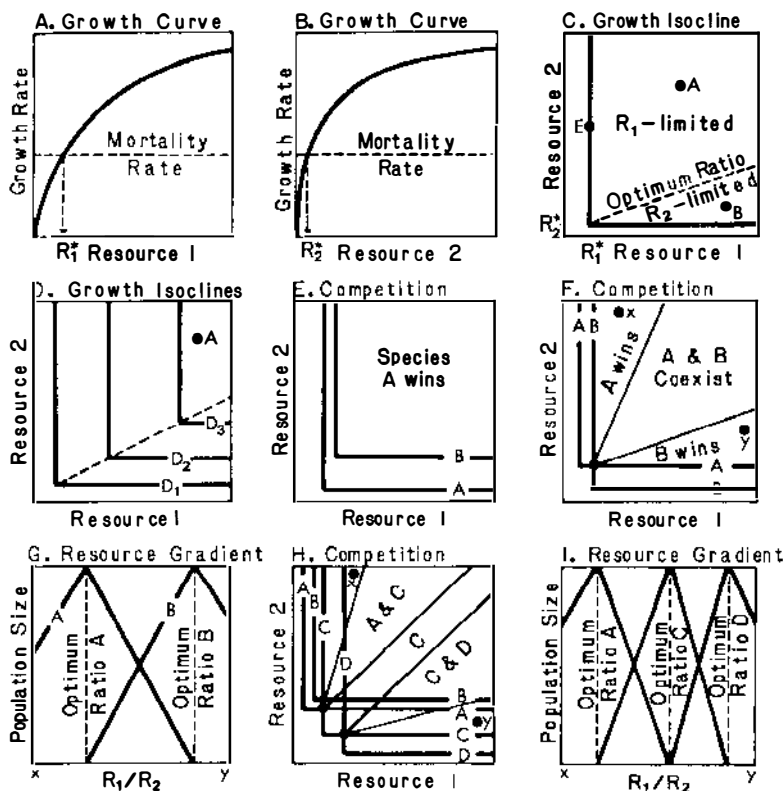


Figure 1 The various parts of this figure illustrate the elements of resource competition theory. See text for details.

The Monod model can only be used to predict the dynamics and eventual long-term outcome of interspecific competition for resources when it is combined with information on the mortality (or loss) rate experienced by each algal species (38), and on the supply rate (or turnover rate) of each limiting resource (112, 113, 114). At equilibrium (nonequilibrium conditions are discussed below), the reproductive rate of a population will balance its mortality rate, and the supply rate of each resource will balance consumption. The species shown in Figure 1A and B, living in a habitat where it experienced the mortality rate shown, could only maintain a stable population if it had at least R_1^* of Resource 1 and R_2^* of Resource 2. At equilibrium the limiting resource would be reduced to R^* , at which point its supply rate would balance its consumption rate. For a chemostat experiment, R^* would be the residual amount of R once an equilibrium had been established with R as the limiting resource.

Theory states that R^* is the single parameter needed to predict the long-term equilibrium outcome of competition among any number of species that are all limited by the same resource (4, 5, 31, 76), and that the one species with the lowest R^* should displace all competitors. Several experiments have supported this prediction (25, 111, 113, 114, 116, 127).

The response of a species to two limiting resources can be illustrated using resource-dependent growth isoclines (112, 114). Figure 1C shows the isocline for the species of Figure 1A and B. This isocline states the amounts of R_1 and R_2 required for this species to maintain a stable population at this mortality rate. The dashed line in Figure 1C represents the optimum ratio of the two resources [i.e. the ratio in which the species consumes the two resources (114)], which is assumed to be a species-specific constant under a given set of conditions (see Figure 4C for clonal variations).

The growth isocline of Figure 1C shows the combination of R_1 and R_2 for which the reproductive rate of this species will equal its mortality rate. Habitats with higher resource availabilities (outside the isocline) will lead to increases in population size, and habitats with resource availabilities inside the isocline will lead to decreases. The species would be limited by R_1 if it were in a habitat with a resource supply point (see 112, 114) in the region labeled A, and by R_2 in region B. At equilibrium for resource supply point A, R_1 and R_2 would be reduced (along a slope equal to the optimum ratio) down to the point on the isocline indicated by an E, where resource consumption would exactly balance resource supply and reproduction would balance mortality. If mortality rate (D) were increased, the position of the isocline would be moved out further from the origin, as illustrated in Figure 1D, because a species requires more resources to reproduce more quickly.

If two species compete for two resources, the relative positions of their isoclines and their optimal resource ratios determine the conditions under which neither species can exist, one or the other is competitively dominant, or the two species stably coexist (55, 112–114). There are four distinct cases of resource competition between two species (112). Two of these are illustrated. If the isoclines of the two species do not cross (Figure 1E), the species whose isocline is closer to the origin (i.e. lower R^* for both resources) will competitively displace the other species. If the isoclines cross, the point at which they cross is a two-species equilibrium point, which may be locally stable or unstable (112). Figure 1F illustrates a stable equilibrium and shows which resource supply points lead to dominance by species A, coexistence of both species, or dominance by species B. Figure 1G demonstrates that species A and B should be separated along a resource ratio gradient (112, 114), with species A dominant at low supply ratios of $R_1 : R_2$ and species B dominant at high supply ratios of $R_1 : R_2$.

This approach may be used to predict the outcome of resource competition among many species competing for two resources. In Figure 1H there are two two-species equilibrium points for the four species shown. Figure 1I gives the relative abundances of these competing species along a resource ratio gradient. It can be seen that Species B is eliminated because the other species can reduce the resources below the R^* 's for Species B. Figure 1H shows that R_1^* of Species A is lower than R_1^* for Species C, which is lower than R_1^* for Species D. The values of R_2^* for each species are in the reverse order. This model has proven useful in predicting the long-term outcome of interspecific competition for two limiting nutrients (29, 112–114).

The various parts of Figure 1 illustrate the most basic elements of a resource-based theory of interspecific competition. The graphs illustrate the long-term, equilibrium outcome of interspecific competition, but give no feeling for dynamics of competition. The dynamics can be predicted only when explicit equations are solved numerically (e.g. 113, 116).

How may the model discussed above—expressed either as differential equations or graphically—be applied to a natural phytoplankton community? First, it is necessary to know exactly which resources limit the growth of the species present. Such data can be approximated initially by the measured in situ concentrations and ratios of resources. However, as can be deduced from Figure 1D, relatively high in situ concentrations do not necessarily mean that a resource is not limiting; a high mortality rate can cause a high equilibrium availability of the resource. Only resource-addition experiments followed by relatively long-term observations of the dynamics of the major species will unequivocally demonstrate which resources are limiting to which species. Second, it is necessary to know the in situ mortality or loss rate experienced by each species (38). There are many reasons to expect that different species will experience different loss rates, and thus an average loss rate for the total phytoplankton may give little insight into the processes controlling the species composition and diversity of the phytoplankton. Third, it is necessary to know the dependence of the reproductive rate of each species on the availability of each potentially limiting resource. This is best done by isolating the major species and characterizing their requirements under controlled laboratory conditions. It is possible to gain a rough idea of their relative resource requirements by growing a natural assemblage at a low initial density in various defined media and observing the growth rates of the major species under conditions of limiting N, P, Si, or light, etc, for several different levels of each limiting resource. Fourth, it is necessary to know the in situ rate of supply of each limiting resource. This has proven to be a difficult task (36, 37, 51, 52, 84), but it is an essential part of understanding the dynamics of natural phytoplankton communities. It may be possible to approximate the relative rates of resource supply using

either ratios of ambient resource concentrations or ratios of the total amounts of each resource in the euphotic zone. If such ratios are strongly correlated with the ratios of resource supply rates, they could be used to determine whether the observed patterns of species dominances in a lake were qualitatively consistent with the pattern predicted from their physiology. An example is given in Figure 2 for four species of Lake Michigan diatoms. Laboratory studies of their requirements for Si and P (Table 1) and laboratory competition experiments (111, 112, 115), predict that *Cyclotella meneghiniana* should be dominant at low Si:P ratios, and that *Fragilaria*, *Asterionella*, and *Synedra* should be more dominant at higher Si:P ratios. An analysis of Kopczynska's (47) field data for the region in which the Grand River flows into Lake Michigan is in general agreement with this prediction (114). The transition from relative dominance by *Cyclotella* to relative dominance by one of the other species occurs at an Si:P ratio approximately ten times that predicted by the physiology of these species. This may be because ratios of ambient Si:P, though correlated with ratios of Si:P supply rates, greatly underestimate the resupply rate of P compared to Si (114). Such a correlation between laboratory predictions and field

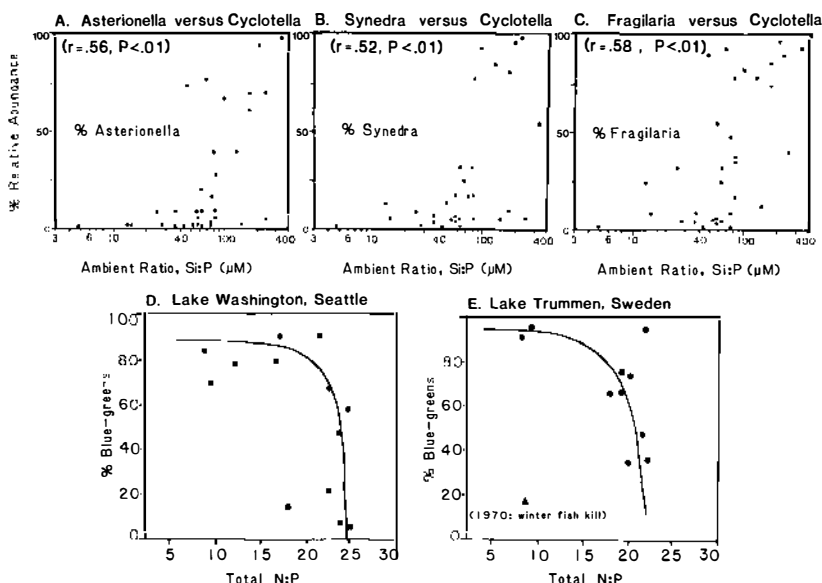


Figure 2 The abundance of *Asterionella* (part A), *Synedra* (part B), and *Fragilaria* (part C) relative to the total abundance of that species and *Cyclotella*, in near-shore samples of Lake Michigan (114, 47). Parts D and E: Percent average annual abundance of blue-green algae compared to annual ratio of total nitrogen (TN) to total phosphorus (TP) in lakes Washington and Trummen [Val H. Smith, personal communication; (114)].

observations can also be explained by other hypotheses, for many other factors vary along the gradient Kopczynska studied. Only experimental manipulations of the natural assemblages from various points along this gradient will distinguish among the competing hypotheses.

Consider also the question of the relative abundances of blue-green algae (which are often capable of fixing atmospheric nitrogen) and other algal species. According to resource competition theory, nitrogen-fixing algae should dominate lakes when nitrogen is limiting. Assuming that phosphorus and nitrogen limit many algae in lakes, blue-green algae should dominate lakes when N:P ratios are low but other types should dominate when they are high. Figures 2D and E show that this general pattern was observed in two different lakes [V. H. Smith, personal communication; (114)]. It has also been observed in experimentally manipulated lakes (22, 97). Similarly, diatoms require silica for growth but green and blue-green algae do not. When silica and phosphorus are the main limiting nutrients in lakes, diatoms should be rare when Si:P ratios are low and should dominate when they are high, if diatoms are better competitors for P than green or blue-green algae. The physiological studies reviewed in Table 1 suggest this may be so.

Another problem is encountered when one tries to apply this (or any other) theory to natural phytoplankton assemblages. Theories often assume spatially and temporally homogeneous habitats, whereas real habitats are structured in space and time (3). Theories that ignore spatial and temporal structure are simpler and allow determination of the extent to which observed patterns in algal diversity and abundance can be explained without invoking these complications. Perhaps useful to the study of patterns in the relative abundance of various pairs of species or taxonomic groups (as in Figure 2), this approach will probably be less so when whole assemblages are considered. This is because the resource competition theory reviewed above predicts that no more species can stably coexist at equilibrium than there are limiting resources (4, 5, 56, 114, 121). However, the addition of spatial structure, temporal structure, or trophic structure leads to the prediction that an unlimited number of species can stably coexist on a few limiting resources (114).

SPATIAL AND TEMPORAL HETEROGENEITY

Numerous studies have demonstrated patchiness in nutrient and algal distributions in pelagic environments (64, 69, 83, 86, 93, 122). These studies reveal patterns of heterogeneity on numerous scales of distance and time.

Table 1 The Monod growth constants (r , day⁻¹; K , μ M) and the calculated R^* values (μ M)^a

	°C	Phosphate			Silicate			Ref
		r (day ⁻¹)	K (μM)	R* (μM)	r (day ⁻¹)	K (+T) (μM)	R* (μM)	
Diatoms:								
<i>Synedra filiformis</i>	20	0.65	0.003	0.0005	1.1	19.7	1.95	113
<i>Synedra ulna</i>	8				0.16	4.9 + 0.2	8.37	116
	13				0.71	3.8 + 0.3	0.92	116
	20				0.65	4.0 + 0.6	1.33	116
	24				0.78	4.4 + 0.3	0.95	116
<i>Asterionella formosa</i>	20	0.59	0.006	0.0012	0.78	2.2	0.32	113
	20	0.90	0.02	0.0025				7
	20	0.61	0.02	0.0039	0.73	3.94	0.63	115
	20	0.67	0.07	0.0123	0.81	2.91	0.41	29
	20				0.77	1.48 + .45	0.67	40
	20				0.42	0.68 + .41	0.62	40
	4				0.35	1.3 + 0.6	1.12	116
	8				0.52	1.6 + 0.2	0.58	116
	13				0.79	2.5 + 0.2	0.56	116
	20				0.73	3.7 + 0.1	0.69	116
	24				0.66	9.3 + 0.9	2.56	116
<i>Fragilaria crotonensis</i>	20	0.80	0.011	0.0016	0.62	1.5	0.29	113
<i>Tabellaria flocculosa</i>	20	0.36	0.008	0.0031	0.74	19.0	2.97	113
<i>Diatoma elongatum</i>	20	0.48	0.02	0.0053	0.85	1.51	0.20	42
<i>Nitzschia acicularis</i>	25	1.30	0.48	0.04				7
<i>Cyclotella meneghiniana</i>	20	0.54	0.25	0.057	0.92	1.44	0.18	115
<i>Stephanodiscus minutus</i>	10	0.36 ^b	0.13 ^b	0.050	0.71	0.31	0.05	66
					0.86	0.68	0.09	66
	15				0.80	1.03	0.15	66
					0.85	0.12	0.02	66
	20	0.50 ^b	0.14 ^b	0.035	0.75	0.88	0.14	66
Blue-Green Algae:					1.29	1.24	0.10	66
<i>Oscillatoria agardhii</i>	15	0.65	0.032	0.0058				2
	20	0.56	0.006	0.0013				2
	25	0.54	0.035	0.0080				2
	20	0.86	0.03	0.0039				120
<i>Microcystis aeruginosa</i>	20	0.25	0.19	0.127				29
Green Algae:								
<i>Volvox aureus</i>	10	0.31	0.23	0.110				101
	15	0.38	0.26	0.093				101
	20	0.69	1.22	0.207				101
	25	0.51	0.62	0.151				101
	30	0.44	0.20	0.059				101
<i>Volvox globator</i>	10	0.14	0.46	1.15				101
	15	0.43	1.24	0.376				101
	20	0.43	1.89	0.573				101
	25	0.51	1.07	0.261				101

^a For phosphorus (P*) and silicon (Si*) for selected freshwater phytoplankton species. The equilibrium mortality rate (D) is 0.1 day⁻¹. $R^* = T + KD/r - D$ (where T is the threshold concentration if different from 0).

^b Unpublished data on same clone.

Of all the heterogeneity that exists in pelagic environments, what aspects of it are important to phytoplankton?

Heterogeneity has typically been classified as being either spatial or temporal. This definition is suitable for sessile organisms (e.g. terrestrial plants or intertidal invertebrates) but is not as useful for organisms living in a fluid medium (26). The most important aspect of heterogeneity is the focus on individuals and what they experience during a given period. To apply these concepts to algal communities, it is necessary to consider three factors. First, all phytoplankton are motile. They may be actively motile via flagella or passively motile via sinking or gas vacuoles (23, 104, 117). Second, nutrient uptake is not directly coupled to reproduction. Individuals are capable of acquiring nutrients to use for future reproduction (11, 15, 18). Third, the water column is heterogeneous. The heterogeneity comes from large-scale depth gradients in nutrients and light; from small-scale patchiness caused by turbulent upwelling, shearing associated with wind-driven mixing, and thermal mixing caused by differential heating and cooling; and from very small-scale patchiness caused by fish and zooplankton excretion and in situ decay of organisms. Thus individual algal cells or colonies will experience different rates of resource supply at any given moment. However, the reproductive rate of an individual algal cell represents, to some extent, an integration of resource concentrations experienced during a time interval at least as long as the time since the last reproductive event. Much of the variation experienced by individual algal cells may be unimportant to their long-term reproductive rate because mixing processes, motility, and cellular nutrient stores allow them to "average out" much of the resource heterogeneity they experience. However, such averaging would not eliminate the heterogeneity of the water column. Even allowing for the averaging effects, different individuals in a population will likely have different reproductive rates. The *variance* in reproductive rates among individuals is the true measure of the effective amount of resource heterogeneity in an aquatic habitat. Such differences in reproductive rates could be caused by two processes: Individual algal cells or colonies could experience different average rates of resource supply, or individual algal cells experiencing the same average rates of resource supply could respond differently because of the temporal pattern of resource variation around the mean. Let's call the first component spatial heterogeneity and the second component temporal heterogeneity. Both must be defined on the basis of individual-to-individual differences in resource supply rates over a period approximately equal to the time between reproductive periods—i.e. on a time scale on the order of the doubling time of a population. How can such spatial and temporal heterogeneity be added to models of resource competition?

Spatial heterogeneity is added to the equilibrium model of Figure 1 by representing both the average rate of resource supply and the spatial variation in average resource supply as experienced by different individuals of a species (112, 114). The isoclines of Figure 3A show a community of four species competing for two resources. A habitat with average supply rates at point 1 would be predicted to be dominated by species B and C, with species A and D extinct. If there were sufficient spatial heterogeneity to have a resource supply point distribution bounded by the circle around the average supply point at 1, all four species would be able to coexist in this habitat (112, 114). Thus, the addition of spatial heterogeneity would allow more species to coexist than there are limiting resources. If habitat 1 were enriched with equal quantities of R_1 and R_2 to give an average supply point at 2, with no effect on the heterogeneity, the habitat could only support two species, suggesting that enrichment should lead to decreased species diversity (112, 114).

Figure 3A can be used to make an additional point. Aquatic ecologists often incorrectly state that a particular lake is "phosphorus limited" or "nitrogen limited." However, if a spatially homogeneous lake had resource supply point 2, species B and C would be coexisting with species B limited by R_1 and species C limited by R_2 . If the lake had the spatial heterogeneity indicated by the circle around point 2, most individuals of species B would be limited by R_2 , but some would be limited by R_1 . The converse would hold for species C. Thus individual algae—not lakes—are limited by a particular nutrient. To say that a particular lake is limited by one particular nutrient is a logical error that may have profound effects on phytoplankton research.

Temporal heterogeneity may seem to be a more difficult matter to include in the "equilibrium" models developed above, because it is inherently "nonequilibrium". However, analyses by Armstrong & McGehee (4, 5) and Levins (57) have shown how temporal heterogeneity may be included. Consider the two species of Figure 3B. The growth response of species A to the average availability of R , \bar{R} , is sigmoid, whereas that of species B is Monod. If these two species competed for this resource in a nonfluctuating habitat, and both experienced the mortality rate shown, species B would competitively displace species A because R_B^* is less than R_A^* [Figure 3B; (111, 114)]. If there were fluctuations in the resource level, the long-term average growth rate of each species would *not* be equal to the growth rate calculated from the long-term average concentration, because the growth curves are nonlinear (5, 57, 114). Increased fluctuations, as measured by the variance in R [$\text{Var}(R)$], would lead to increased per individual reproductive rates for species A and to decreased reproductive rates for species B, even with the long-term average resource concentration held constant

(Figure 3C). The increase in the growth rate of species A with resource fluctuations means that $\text{Var}(R)$ is functionally another resource for species A, while the decrease in growth of species B with $\text{Var}(R)$ means that $\text{Var}(R)$ is a limiting factor (56) for species B. There is a level of \bar{R} and $\text{Var}(R)$ at which the reproductive rate of each species equals its mortality rate, thus allowing both species to stably persist on "one" limiting resource [Figure 3D; (5, 57)]. Such a persistence is "nonequilibrium" in the sense that the coexistence is allowed by resource fluctuations. However, the relationships that allow long-term persistence of these two species are easily illustrated using resource-dependent growth isoclines, as in Figure 3D. Both Levins (57) and Armstrong & McGehee (4, 5) have demonstrated mathematically that an unlimited number of species can coexist on one or two limiting resources as long as species have nonlinear responses and there are resource fluctuations.

These analyses reduce the question of temporal heterogeneity to its most basic element, which has been overlooked by those working on the ecological effects of temporal heterogeneity. The central piece of information needed to predict the long-term outcome of competition in fluctuating environments is the effect of resource fluctuation on the *long-term* reproductive rates of species. No studies show such data. The increased interest in temporal heterogeneity has led to finer and finer time scale investigations of nutrient uptake and to increasingly complex models of algal physiology. Such models may prove useful in understanding what factors cause nonlinear growth responses, but they are not the best first step in determining

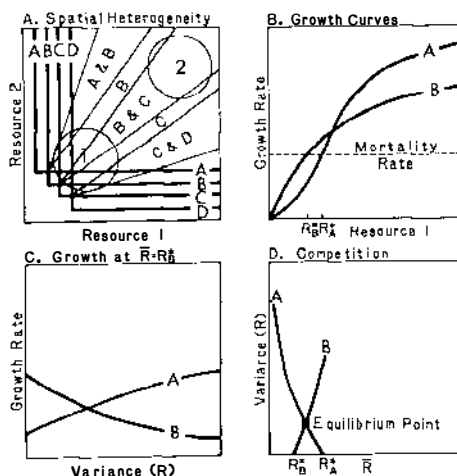


Figure 3 A: Spatial heterogeneity can allow many species to coexist on two or more limiting resources. Note that resource fluctuations [$\text{Var}(R)$] can be responded to as if they were a resource (part C, species A) or a limiting factor (part C, species B).

whether resource fluctuations can influence resource competition à la Armstrong & McGehee and Levins. The ultimate prediction hinges on the dependence of the reproductive rate on the magnitude or period of fluctuations. This should be observed directly in any test of this model. The interesting data of Turpin, Harrison, and Parslow (118, 119) seem strongly suggestive of the possible effects of resource fluctuations on competition, and studies such as this should be refined and expanded.

These theoretical considerations of the mechanisms of competition and coexistence in phytoplankton lead us to conclude that the paradox of the plankton (34) is now a dead issue. So, too, should be the question of the factors allowing the local coexistence of a particular number of species. The distinction between equilibrium and nonequilibrium approaches fades once it is realized that algae respond to resource fluctuations as if the fluctuations were either another resource or a limiting factor. The long-term outcome of competition for a fluctuating resource can be predicted using the same approach used to predict the outcome of competition for any other type of resource (Figure 3B–D). For this reason, and because it is virtually impossible to separate spatial and temporal heterogeneity in a pelagic environment (26), we suggest that the dichotomy between equilibrium and nonequilibrium approaches is of limited utility. We suggest that phytoplankton ecology concentrate, instead, on the role of resources in determining patterns that span spatial and temporal scales great enough to integrate the effects of small-scale temporal and spatial heterogeneity.

SUCCESSION

Phytoplankton ecologists have long been fascinated by the repeated seasonal fluctuations of algae (35, 79, 80, 123). The patterns are usually similar from year to year and among lakes of similar trophic status in a region and are often characterized by only a few dominant species (88). This suggests that a few basic processes may control the general successional sequence in lakes. These processes are usually subdivided into two components—allogenic and autogenic factors (58, 105). Allogenic factors are water chemistry, turbulence, temperature, and other external factors. Autogenic factors are species physiological and life-history characteristics, competition, predation, parasitism, allelopathy, and other factors under biological control. The degree to which external control or species interactions are more important in causing succession is a matter of debate (26, 44, 58, 87, 88, 96, 105). Factors that experimental manipulations demonstrate to be major controlling variables should be studied first. Successful explanations are most likely to come from mechanistic approaches that give testable predictions. Initial work might best focus on factors that cause dominance of particular species

rather than attempt to explain the complexity of population dynamics during succession.

Reynolds (88) argued that the interactions of only two major factors, nutrient availability and column stability, can explain observed community structure changes in lakes and experimental tubes in England. Zevenboom & Mur (126) examined the succession of algae in Dutch lakes based on the physiological responses of the three major species to light, phosphorus, and nitrogen limitation. They concluded that, although it was difficult quantitatively to extrapolate laboratory results to the field, the qualitative predictions provided significant insights into the mechanisms responsible for the species shifts.

Study of succession will require a synthesis of work on the physiological ecology of major algal species with that on the mechanisms controlling the loss rates and rates of nutrient supply and cycling within the water column. It will thus require a marriage of what have often been disparate approaches in ecology—those of the population ecologist and the ecosystem ecologist. While it is premature to make quantitative predictions about successional change in nature, we believe it is possible to use the graphical-mechanistic approach to formulate testable hypotheses about succession. We give three examples of this approach.

Competitive Interactions with Changing Resource Ratios

Several authors (26, 105) have recently argued that the single limiting nutrient approach is too simplistic to explain a phenomenon as complex as succession. This is likely true, but it does not follow that the resource approach should be discarded because the simplest case does not work. We argue that different combinations (ratios) of potentially limiting resources have different effects on phytoplankton community structure [Tilman's Resource Ratio Hypothesis (114); 22, 43, 44, 89, 90, 111–113, 116, 119] because not all species have the same growth responses to low levels of different resources (Table 1). Figure 4A shows a model of the physiological characteristics of two species, a diatom (*Asterionella formosa*) and a blue-green (*Oscillatoria agardhii*), under conditions of potential limitation by phosphorus and silicon (for the diatom). *A. formosa* would dominate at time 1, when the supply rate of phosphate was low relative to that of silicate. Increased rates of phosphate supply would lead to coexistence of the two species at time 2, and even further increases in phosphate supply would lead to dominance by *O. agardhii*. *A. formosa* would be eliminated because of severe silicon limitation. A similar relationship is illustrated (Figure 4B) for N and P limitation of two blue-green algae, *O. agardhii* and *Anabaena flos-aquae*. Increased rates of phosphorus supply would lead to a succession from *Oscillatoria* to *Anabaena*. Lake Mjösa, Norway, had a successional sequence from *O. agardhii* to *A. flos-aquae* (30) under conditions of cultural

eutrophication (increased phosphorus supply). The theory in Figure 4B may explain this shift. This could be tested initially by determining the relative requirements of these two species for N and P to see if their requirements are as shown in Figure 4B. If they are not, this hypothesis could be easily rejected.

Kilham (39) reported a successional sequence from dominance by *Melosira* to *Asterionella* to *Tabellaria* to *Stephanodiscus*. Because it occurred as silicate levels declined, he suggested that this sequence could be explained if the later species had increasingly lower silicate requirements for growth. It now seems that this hypothesis should be expanded to include changes in the ratio of Si:P supply rates in the water column. If Si:P supply ratios decline through the season, the diatom Si and P requirements of Figure 4C would predict a seasonal succession from *Synedra* to *Asterionella* to *Fragilaria* to *Diatoma* to *Stephanodiscus*, which is not inconsistent with Kilham's original observations (39).

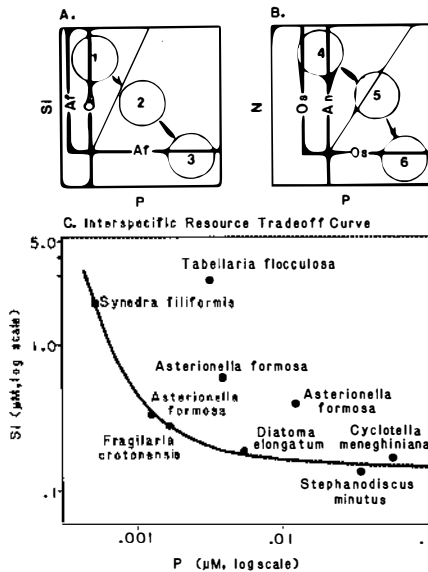


Figure 4 A: Hypothetical cases of competition between *Asterionella formosa* (Af) and *Oscillatoria agardhii* (Os) for silicate and phosphate. If silicate declines relative to P, there should be a succession from *Asterionella* to *Oscillatoria*. B: A similar hypothetical case of competition between two species for N and P. An increase in P relative to N should cause a succession from *Oscillatoria* (Os) to *Anabaena*. (An) C: Some of the data reviewed in Table 1 have been graphed to illustrate the interspecific tradeoffs in diatom competitive abilities for silicate and phosphate. Note that the superior competitor for phosphate at 20°C (*Synedra*) is the most inferior competitor for silicate. Similarly, *Stephanodiscus* is the best competitor for silicate but the worst competitor for phosphate.

Selective Loss Rate Increasing For One Species

The loss rates experienced by a species are just as important as growth rates in determining species compositions of phytoplankton communities. The factors responsible for changes in loss rates are often difficult to determine. Sinking (8, 117), grazing (62), parasitism (6), and changes in mixing (88) are all possible causes. Figure 1F shows two species competing for two resources and assumes that the two species have similar loss rates. As already discussed, there is a range of $R_1 : R_2$ ratios for which these species may coexist. However, if the loss rate for species B increased (owing perhaps to selective grazing or parasitism), then it would need a great deal more of each resource in order to maintain a population. Figure 1E illustrates a case in which the increased loss rate for species B would lead to its extinction. Clearly, seasonal fluctuations in loss rates could lead to successional changes.

Temperature has long been considered a primary factor in determining phytoplankton succession because of its action on maximum growth rates (reviewed in 21, 59, 105). More recently the emphasis has shifted to temperature effects on the physiology of resource utilization [(59, 66, 91, 116, 124); Table 1.] There are not enough data on any pair of species for two resources under different temperature conditions to enable us to construct a temperature-dependent resource-growth isocline diagram. However, the effects can easily be illustrated using the interactions between a single resource and temperature. Figure 5A shows the temperature dependence of the resource requirements (R^*) of several hypothetical species. Because the species with the lowest R^* should be the superior competitor at a given temperature, the curves predict that species A should dominate at low temperature, followed by species B and C as temperature increases. The implications of such relationships for succession are clear: Temperature tends to increase during the growing season, and this could lead to a successional sequence from species A to B to C. A similar pattern could occur with the relationships in Figure 5A if the allogenic factor were pH, amount of wind-driven mixing (65, 88), total alkalinity, SO_4^{2-} , etc. Figure 5B illustrates an experimental test of this theory (116) in which the temperature dependence of the silicate requirements of two diatoms predicted the outcome of competition along a temperature gradient.

The major patterns of algal seasonal succession may be largely explained by the interactions between supplies of P, N, it is not possible to illustrate the interactions among four factors graphically, but it is an easy matter to express these relationships mathematically and to solve the equations numerically to determine the predicted seasonal pattern of succession. If the findings of Tilman et al (116) prove general, it may be that temperature affects mainly the maximal growth rate of a

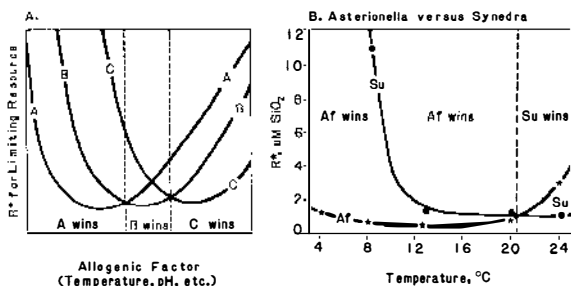


Figure 5 A: Competition for one limiting resource in relation to an allogenic factor such as temperature or pH. According to theory, the one species with the lowest requirement (R^*) for the resource at a given level of the allogenic factor should competitively displace the other species. B: A test of this theory was performed using *Asterionella formosa* (Af) and *Synedra ulna* (Su) competing for silicate at different temperatures. The outcomes of competition generally agreed with predictions (116).

species, not its half-saturation constant for a nutrient. This would considerably reduce the amount of experimentation required to develop such a mechanistic approach to algal succession.

TROPHIC STRUCTURE AND FOOD CHAINS

The species composition and total biomass of phytoplankton communities depend to a great extent on interrelations between the phytoplankton community and the rest of the food chain. The outcome of resource competition is determined by the physiological properties of the algae themselves, the supply rates and ratios of potentially limiting nutrients, and the mortality rates (often a result of zooplankton grazing or sinking) experienced by particular species of algae. In many aquatic systems zooplankton grazing is responsible for a large fraction of the mortality. Selective grazing that results in the differential mortality of phytoplankton is well documented (24, 85), but differential nutrient regeneration and nutrient patchiness caused by zooplankton may ultimately prove to be more important mechanisms by which zooplankton affect phytoplankton (44, 53). In some lakes nutrients regenerated by zooplankton in the epilimnion supply most of the nutritional requirements of phytoplankton populations during the summer (51, 52). If some nutrients (e.g. phosphorus) are regenerated more rapidly than others, zooplankton may significantly affect phytoplankton community structure by changing both nutrient supply rates and ratios.

The biomass of phytoplankton communities is primarily a function of the rates of nutrient supply and algal loss. If mortality rates are low, nutrients supplied to the system will accumulate as algal biomass, and ambient nutrient levels in the system will remain low. Eventually the phytoplankton may

become light-limited as the supply of nutrients to the system is increased (126). In a system with similar nutrient supply rates, but considerably higher rates of algal mortality, algal biomass would not accumulate, ambient nutrient concentrations would be higher, and the division rates of individual species of algae would increase. These conclusions are derived largely from the behavior of algae in chemostats, but they agree with observations of algal populations in nature. The classical positive relationship, for example, between summer chlorophyll *a* concentrations and total phosphorus at spring overturn is a result of nutrients' being accumulated as biomass (17). The relationship holds because algal mortality rates in many temperate lakes are low. If algal mortality rates were sufficiently high, biomass would not accumulate and the relationship between chlorophyll *a* and phosphorus would change.

Smith (106) used a simple mathematical model of a theoretical ecosystem containing either three or four trophic levels to study the effects of nutrient enrichment in aquatic systems. He examined the consequences of using different rate constants, of varying the number of trophic levels, and of increasing nutrient density. His results were strongly dependent on the number of trophic levels modeled and much less dependent on the rate constants used. Shapiro, Lamarra, and Lynch (62, 102, 103), have demonstrated from field observations and experiments that trophic structure influences the species composition of algae in lakes.

Hecky (28) has shown that the biomass pyramids determined for a number of tropical lakes conform well to Smith's (106) predictions. Lake George, Uganda, is an enriched aquatic ecosystem comprised of three major trophic levels: primary producers (phytoplankton), herbivores (zooplankton and fish), and predators (zooplankton, insect larvae, and fish). Nutrient enrichment accumulates primarily in the first trophic level (phytoplankton), and only slight increases are shown in the third trophic level (predators). The biomass of the second trophic level (herbivores) is largely unaffected by enrichment. However, enrichment increases the turnover rate of the herbivores at the same time it decreases the turnover rate of phytoplankton.

In an ecosystem with four major trophic levels (secondary predators are present), the biomass pyramid often has a narrow base (106). At high levels of enrichment, phytoplankton biomass is reduced and most of the added nutrients accumulate as free resource, but there are increases in the biomass of the herbivores and the secondary predators. Under these conditions the turnover rates of the phytoplankton are maximized at high levels of enrichment. The pelagic ecosystem of Lake Tanganyika is comprised of four trophic levels and seems to behave as predicted by Smith's model (28).

These studies suggest that the trophic structure of aquatic ecosystems plays a major role in phytoplankton ecology. The one divergent point in Figure 2E emphasizes this point. The change in the trophic structure of

Lake Trummen caused by a winter fish kill (V. H. Smith, personal communication) greatly changed the relationship between N:P ratios and blue-green dominance.

CONCLUSIONS

First, more experimental, manipulative studies must be done to determine what relationships might exist between correlations based on field observations and the causative mechanisms controlling algal community composition. Second, although we suggest that resource competition among algal species is the central mechanism controlling the composition of phytoplankton communities, the approach will probably prove to be of limited utility for natural assemblages until it has been broadened to include the effects of factors such as temperature and pH. Third, we suggest that the spatial and temporal heterogeneity of pelagic environments will prevent us from meaningfully addressing questions on short time scales or small spatial scales. Instead of concentrating on causes of species diversity, workers should emphasize seasonal population dynamics and succession. Further, we believe that such an emphasis will require a broadening of the aquatic ecologist's perspective to include processes at other trophic levels. Thus we suggest that a synthesis of approaches used by population ecologists and ecosystem ecologists is needed before there can be significant advances in our understanding of phytoplankton ecology.

ACKNOWLEDGMENTS

This was prepared while DT was supported by NSF grant DEB-7904250 and by Sea Grant DOC/NA81AA-D-00114. This is contribution No. 115 from the Minnesota Sea Grant Institute. SSK and PK were supported by NSF grants OCE78-27016 and OCE81-17377. We thank Laura Carlson for typing the manuscript and Sue McEachran for preparing the figures and references.

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