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Hypothesized resource relationships among African planktonic diatoms

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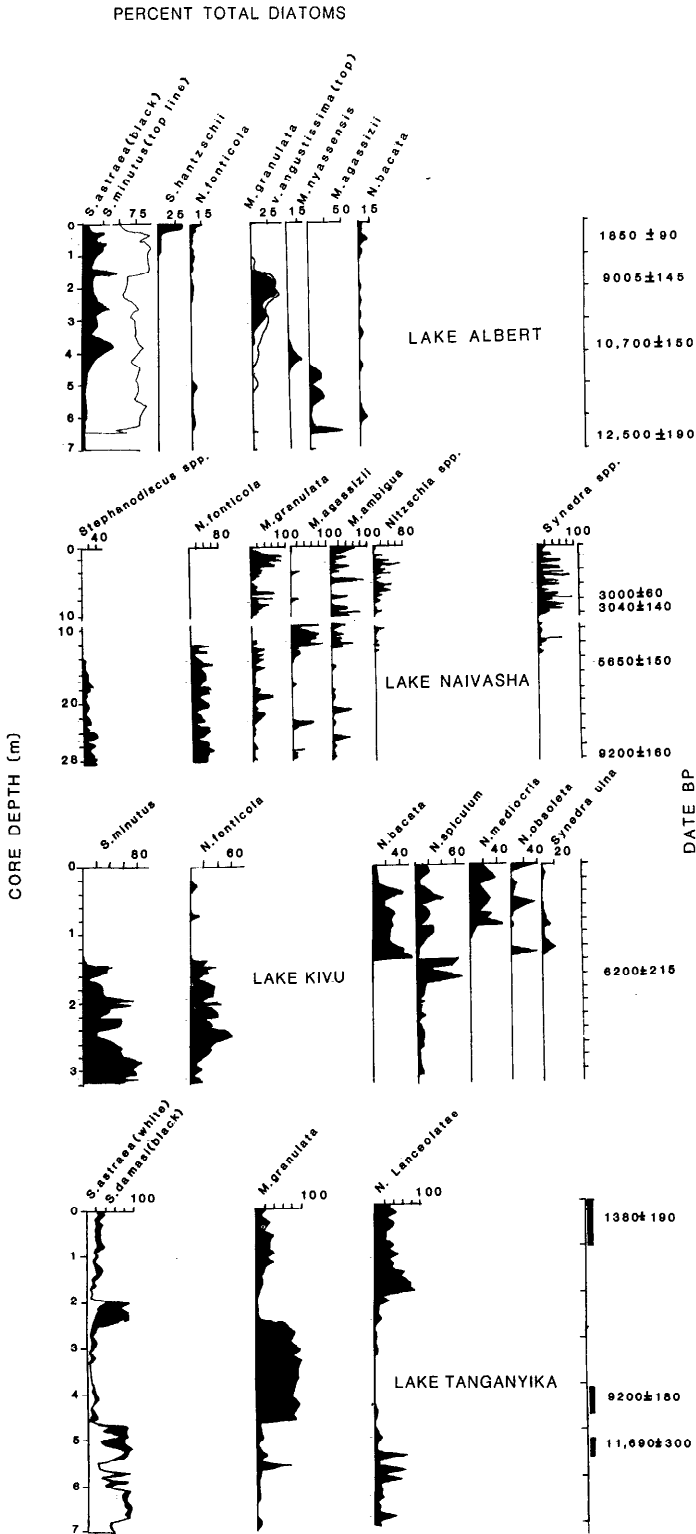
Abstract

Several hypotheses are advanced for resource relationships among planktonic diatoms in African freshwater lakes that are consistent with the light and nutrient conditions of the lakes and the extant and fossil distributions of the diatom species in them. The hypotheses are all testable and are potentially powerful tools for interpreting past climatic conditions. A ranking is proposed along a Si:P gradient: at the high end are the planktonic *Synedra* spp. with the highest Si requirements and lowest P requirements (high Si:P), the planktonic *Nitzschia* spp. are intermediate, and the *Stephanodiscus* spp. are at the low end with the lowest Si requirements and highest P requirements (low Si:P). *Melosira* species may be ranked along a light:P gradient. We suggest that *Melosira distans* and *Melosira ambigua* grow under high light and have low P requirements, *Melosira agassizii* and *Melosira granulata* are intermediate, and *Melosira nyassensis* has the lowest light and highest P requirements. There also appears to be a relationship between pore size and the light regime for growth among the *Melosira* species; thus, *M. distans* and *M. ambigua* have the smallest pores and highest light requirements, *M. nyassensis* has the largest pores and lowest light requirements. *Melosira granulata* is intermediate and seems to be very variable in pore size, depending on the light environment. One diatom, *Nitzschia fonticola*, lives in and on colonies of *Microcystis* and is considered to be an obligate nitrogen heterotroph.

Planktonic diatoms from Africa have long been of interest to diatomists (Müller 1905; Hustedt 1949) and paleoecologists (see Richardson et al. 1978). Many fossil diatom records for sediment cores and exposed diatomite beds from Africa have been used to interpret climatic changes over the last 20,000 years or more. These cores are dominated by a few diatom species, often for thousands of years (Fig. 1). In Lake Albert (=Lake Mobutu Sese Seko), *Stephanodiscus* species have dominated the plankton dia-

tom assemblage for about 12,000 years. In lakes Naivasha, Kivu, and Tanganyika there were several abrupt shifts in dominance, especially about 5,000 B.P., to new species that then persisted for long periods. The challenge is to identify the important features of the ecology of these species in order to provide the most precise reconstruction possible of past conditions in Africa.

We present here several hypotheses concerning resource relationships of planktonic diatoms in African lakes and rivers. These



hypotheses are based on known physiological parameters for similar species from temperate lakes and on distributional and ecological studies of African planktonic diatoms. The underlying mechanism is the relative competitive abilities of different species for phosphorus, silicon, and light (Tilman 1982; Tilman et al. 1982). The hypotheses are falsifiable. Evidence from the literature is presented that we believe builds a strong case in support of these ideas and makes them useful for interpreting changes in planktonic diatom community structure.

African lakes provide a gamut of possibilities for resource limitation. Contrary to the generalization that tropical lakes are nitrogen-limited systems, there appear to be many cases of possible resource limitation by phosphorus, nitrogen, silicon, light, or iron (see Melack et al. 1982). Nitrogen limitation is most often associated with dominance by blue-green algae (Cyanobacteria), and there are numerous cases. In our analyses planktonic diatoms do not appear to be responding to nitrogen limitation as a selective force to any extent, except for species that are obligate nitrogen heterotrophs (e.g. *Nitzschia fonticola*). This impression may change as more data become available on nitrogen requirements of freshwater diatoms. Phosphorus limitation of phytoplankton in African lakes has been documented by Melack et al. (1982) and Kalff (1983). Lakes Malawi and Tanganyika may have periods of low phosphorus availability. Lakes Albert, Malawi, and Tanganyika all have periods of extremely low silicon concentrations which may limit the growth of many species of diatoms (Talling 1963; Talling and Talling 1965; Coulter 1977; Hecky unpubl.). Talling (1966) suggested that iron limitation was a possibility in Lake Victoria.

We will discuss diatom species from lakes that are for the most part large and dilute

so that salinity (major ion) changes are of little importance to species succession in ecological or geological time (cf. Hecky and Kilham 1973 for a review of African saline lakes). The water chemistries of the lakes we will consider are quite similar (Kilham 1971a) with the possible exception of Lake Kivu, although even this lake contains most of the same species of diatoms as the other western rift valley lakes (Hecky and Kling 1986; Hecky and Haberyan in prep.).

Phytoplankton community structure can be affected by herbivorous zooplankton through selective consumption and nutrient regeneration (Sterner 1986), but the net result of these combined processes has not been thoroughly studied, especially in the tropics. Diatoms probably escape grazing to some extent by being outside the optimal size range for the zooplankton (Lehman and Sandgren 1985; Sterner 1986), with the main grazing pressure falling on small green and blue-green algae. It is likely, however, that the zooplankton does provide a source of regenerated nutrients for diatoms and thus contributes to the seasonal evolution of Si:P ratios. Grazing causes rapid regeneration of P while Si losses from the euphotic zone are accelerated by fecal pellet sedimentation (Officer and Ryther 1980).

There are limitations to the data available from Africa used to generate our hypotheses. There are very few data on the resource physiology of any planktonic diatoms from Africa, although there is a measurement for sinking rate of nutrient-replete and phosphorus-starved *Melosira agassizii* (Titman and Kilham 1976). There is a general lack of nutrient data and light measurements in African lakes, especially seasonally, for all but a few cases where phytoplankton populations were followed. Mixing patterns change seasonally in many of the lakes (Talling 1969) and this parameter is important to the ecology of planktonic diatoms, yet

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Fig. 1. Selected stratigraphic records of diatoms in four African lakes. These are tracings from the original diagrams, with the species rearranged for convenience. Some species were omitted. The core from Lake Albert (=Mobutu Sese Seko) is from Harvey (1976), Lake Naivasha is from Richardson and Richardson (1972), and Lake Kivu and Lake Tanganyika are from Hecky and Haberyan (in prep.) and Haberyan (1985). Genera are *Stephanodiscus*, *Melosira*, and *Nitzschia*. N. Lanceolatae refers to long thin species of *Nitzschia* in the Lanceolatae and Nitzschiellae groups within the genus (Hustedt 1949).

turbulence has rarely been measured. Surface sediment samples (Gasse et al. 1983) have been useful to some degree for distributional information, but the importance of seasonal or even decade-long changes is obscured in such material (Bradbury 1975). Modern phytoplankton samples are often limited to single collections of perhaps a few samples over a year or so. Two well studied African lakes, George and Victoria, are atypical to some degree in their stability characteristics and phytoplankton associations (Ganf and Viner 1973; Talling 1966). There are few data on the C, N, Si, and P composition of phytoplankton populations that might provide clues as to the type and degree of resource limitation in particular lakes. All of these limitations are balanced in part by advances in understanding the role that resources play in determining species changes among diatoms (Tilman 1982; Tilman et al. 1982, 1984; Kilham and Kilham 1984; Sommer 1985). We have applied some of the principles outlined in the papers just cited to generate a set of testable resource-related hypotheses about interactions among African planktonic diatoms that may be useful in reconstructing past climatic events or explaining present distributional data.

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Planktonic Synedra and Nitzschia

We will consider the long, slender species of *Nitzschia* and *Synedra* as a group. These include *Nitzschia bacata*, *Nitzschia acicularis*, *Nitzschia spiculum*, *Nitzschia spiculoides*, *Synedra ulna* group, *Synedra acus*

group, *Synedra rumpens*, and other species with similar morphologies. *Synedra berlinensis* is a small diatom (<15 μm long), but it behaves in a manner somewhat similar to the other members of this group (see below). Hustedt (1949) described a large number of *Nitzschia* species from African lakes. Richardson and Richardson (1972) combined these *Nitzschia* species into a group of long types. Despite taxonomic differences these planktonic species appear to have quite similar physiological characteristics.

Planktonic *Synedra* species are the best competitors for phosphorus among all diatoms studied to date (Tilman 1981; Kilham 1984) and also in natural phytoplankton community experiments under P limitation (Sommer 1983, 1985; Smith and Kalff 1983; Tilman et al. 1986; Kilham 1986). *Synedra* species are poor competitors for silicon (Tilman 1981; Kilham 1984) and therefore grow best when Si is not limiting, making them "high Si : P" species (Fig. 2). In experiments using pulsed nutrient additions, Sommer (1985) showed that *Synedra* species maintained relatively constant populations under pulsed P additions, but responded with strong oscillations to pulsed Si additions. *Synedra* species should therefore be most abundant in lakes in which Si loading is high and fairly constant and P loading is very low.

Data on the nutrient physiology of planktonic *Nitzschia* species are not available, but we propose that these species are similar in their physiological characteristics to *Asterionella formosa* and *Fragilaria crotonensis* in temperate lakes, i.e. that they are good at growing at low P supply rates and have moderate requirements for Si (Tilman et al. 1982), making them intermediate between *Synedra* spp. and *Stephanodiscus* spp. with optimal molar Si : P ratios of about 75–150 (Fig. 2). *Nitzschia actinastroides* reacted much like *A. formosa* in the Lake Constance (West Germany) natural community continuous culture experiments of Sommer (1983, 1985). In similar experiments, but with pulsed nutrient additions (Sommer 1985), *N. acicularis* became abundant at moderate to high Si : P ratios. In Lake Ontario, *N. bacata* shows distributional pat-

terns very similar to those of *A. formosa* (Stoermer et al. 1975). We hypothesize that the long, needlelike *Nitzschia* species have fairly high optimal Si:P ratios and fill a niche in tropical lakes similar to that of *A. formosa* and *F. crotonensis* in temperate lakes. It is probable that these latter two species are restricted to lakes with temperatures generally below 20°C (Tilman et al. 1981). *Asterionella formosa* has been reported in Africa in lakes with temperatures below 20°C at elevations above 3,000 m (Hustedt 1949).

The modern distributions of *Synedra* species in African lakes support the hypothesis that these species thrive in high Si:P environments. Lake Naivasha often has blooms of *S. acus* in April–May (Gasse et al. 1983) during the time when P is most limiting (Kalf 1983). The Si concentrations are usually $>400 \mu\text{M}$ (Kilham 1971a; Talling and Talling 1965) and are never limiting. *Synedra ulna* is also abundant during the bloom of *Melosira ambigua* that precedes the *S. acus* flowering, which indicates to us that *S. ulna* has a somewhat higher P requirement (lower Si:P ratio) than *S. acus*. *Synedra acus* is also very abundant in surface sediment samples from lakes Bulera and Luhondo, Rwanda (Gasse pers. comm.). These lakes have very low levels of phosphate ($<0.3 \mu\text{M P}$) and moderately high levels of silicon, especially below 5 m (Damas 1954).

There are two unusual *Synedra* species that have distinctive occurrences. *Synedra berolinensis* is an important planktonic species in Lake George, Uganda (Ganf 1974; see also section on *N. fonticola*). This lake has ambient concentrations $>300 \mu\text{M Si}$, extremely low nitrogen (mostly as NH_4^+ , with daily oscillations with a maximum of $5.0 \mu\text{M N}$ at dawn; no NO_3^-), very low inorganic phosphate ($<0.03 \mu\text{M P}$), and an algal particulate C:P atomic ratio of 300:1 (Viner 1973). Taken together, these figures indicate that both N and P are potentially limiting in Lake George. *Synedra berolinensis* therefore seems to be both a high Si:P and a high Si:N species. *Synedra acus* and *S. ulna* appear to require higher N levels for growth than *S. berolinensis*, which makes them unable to compete in

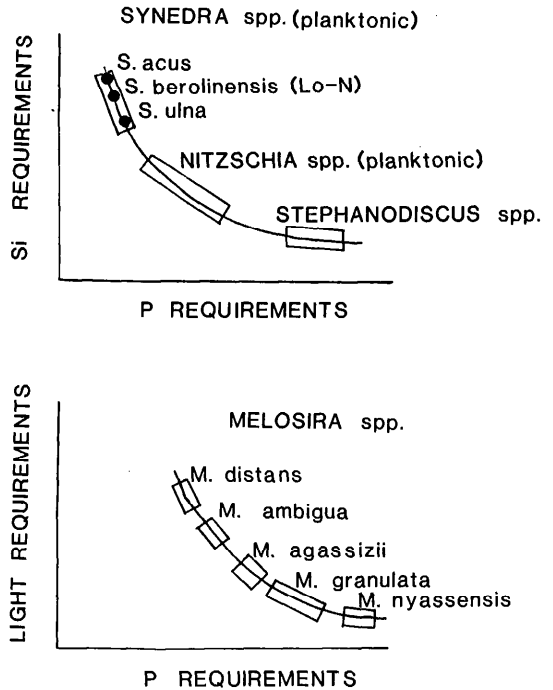


Fig. 2. Hypothesized growth relationships for planktonic diatoms from Africa. The theory and some examples of the physiological mechanisms underlying these curves are given elsewhere (Tilman 1982; Tilman et al. 1982). These tradeoff curves can be evaluated quantitatively in terms of the R^* values for each species and each resource (see Tilman et al. 1982: table 1 and figure 4). R^* is the amount of resource remaining once an equilibrium has been established for a particular limiting resource.

Lake George. The other unusual species is *S. rumpens*. It is very abundant (57% of diatoms) in the surface sediments from Lake Chibwera (Uganda), along with *Melosira granulata* (32%) and *M. ambigua* (10%; Gasse pers. comm.). *Synedra rumpens* is not reported as common in other African lakes, but was the dominant *Synedra* species in the Sunda Lakes, Indonesia (Ruttner 1952).

The long, slender *Nitzschia* species are often abundant in lakes Malawi and Tanganyika (Hecky and Kling 1986), especially during the mixing period of April–September. We can speculate that they are out-competed for Si by *Stephanodiscus* species as the season progresses and the Si supply falls (Hecky and Kling 1986). Coulter (1977) reported values for Lake Tanganyika which give Si:P ratios of about 30:1 for inter-

mediate depths before seasonal mixing, indicating that the supply rates of these nutrients produce moderate Si : P supply ratios as mixing proceeds. We propose that the relatively low Si levels in lakes Tanganyika and Malawi allow *Nitzschia* spp. to dominate over *Synedra* spp. because of lower Si requirements for growth. An isolated bay of Lake Kivu (Kabuno Bay) had *Synedra* and *Nitzschia* species as prominent members of the plankton in March 1972, unlike other areas of the lake at that time (Hecky and Kling 1986). The submixing zone in Kabuno Bay has an Si : P ratio of 420 : 1 (Degens and Kulbicki 1973; the submixing zone is the region below the mixed layer from which nutrients diffuse). Species in these genera may coexist here because of moderate Si : P ratios, with *Synedra* spp. being more Si limited and *Nitzschia* spp. being more P limited. In Lake Albert, *N. bacata* sometimes constituted > 5% of the fossil diatom assemblage during the past 12,000 years (Harvey 1976; Fig. 1), which may indicate slightly higher relative Si : P loadings at times.

Stephanodiscus

The genus *Stephanodiscus* contains many species whose systematic positions are uncertain (Round 1981, 1982; Theriot and Stoermer 1984), but the planktonic species of Africa are probably similar in their physiological ecologies. There are four "species" that are common members of phytoplankton communities, two large ones, *Stephanodiscus astraea* (= *Stephanodiscus rotula*) and *Stephanodiscus damasi*, and two smaller ones, *Stephanodiscus minutus* (= *Stephanodiscus astraea minutula*) and *Stephanodiscus hantzschii*. Kilham (1971b) showed with comparative distributional data that *S. astraea* generally only achieved dominance in lakes with low Si levels and suggested that this species might have efficient utilization kinetics for Si; Mechling and Kilham (1982) showed that *S. minutus* does indeed have a very low growth requirement for Si. Kilham (1984) found that *S. minutus* has a higher growth requirement for P than other planktonic diatoms; we therefore characterize it as a low Si : P species, meaning that it is a good competitor

for Si and a poor competitor for P. Its optimal molar Si : P ratio is about 1.0.

Stephanodiscus species must have a high supply rate of P to become dominant and they can grow successfully under conditions of low Si and low light. They can also grow well with higher Si and light if P is not limiting to their growth. If the Si levels are decreased relative to P supply rates because of increased Si demand caused by diatom growth, then *Stephanodiscus* species can gain control and become dominant as the Si : P supply ratio falls and other diatom species are outcompeted for Si.

The distributional data available for Africa support the hypothesized general physiological characteristics for *Stephanodiscus* species (Fig. 2). Lake Albert (Uganda) has very low Si (<16 μM Si) and relatively high P (>4 μM P) ambient concentrations (Si : P = 0.5–4; Talling 1963), indicating a similar low Si : P ratio for the supply rates of Si and P. The rivers entering Lake Albert come from lakes that are sinks for silicon owing to the sedimentation of diatom frustules (lakes Edward and Kioga/Victoria: Viner 1975; Talling and Talling 1965), so the Si : P supply ratio is reduced in the inflows to Lake Albert. Lake Albert is dominated by *Stephanodiscus* species today (Hecky and Kling 1986) and has been so dominated for the last 12,000 years (Harvey 1976). *Stephanodiscus* species become abundant following blooms of *Nitzschia* species in lakes Malawi and Tanganyika (Hecky and Kling 1986), perhaps as a result of competitive interactions as the Si : P ratio falls.

The niche characteristics that might distinguish among the several "species" of *Stephanodiscus* are unknown. Harvey (1976) found that *S. hantzschii* became more abundant relative to *S. minutus* and *S. astraea* at the top of the sediment core from Lake Albert (<2,000 B.P.). Hecky and Haberyan (in prep.) found that *S. damasi* became dominant several times in a core from Lake Tanganyika, especially about 10,000 and 6,000 B.P. There are no lakes in which *S. hantzschii* or *S. damasi* has been identified as dominant in modern phytoplankton samples from Africa, so clues from their modern distributions are scanty; Gasse et al. (1983), however, suggest that high con-

centrations or proportions of K^+ and Mg^{2+} may favor the growth of *S. damasi*.

Melosira

The genus *Melosira* has many species that are key members of the plankton in Africa (Müller 1905; Huber-Pestalozzi 1942; Hustedt 1949; Talling 1966; Hecky and Kling 1986). The genus is complicated by the use of numerous varietal or status designations within species to distinguish among morphological variants (see Hustedt 1930; Huber-Pestalozzi 1942), usually associated with the degree of silicification and the density of pores (areolae) in the frustule. These taxonomic characters may, of course, prove to be ecologically important. We limit our discussion to five species of *Melosira* which can become common members of the plankton and have often been identified in sediment core material from African lakes (Fig. 1): *Melosira distans*, *M. ambigua*, *M. agassizii*, *M. granulata* and *Melosira nyassensis*. *Melosira agassizii* and *M. nyassensis* are morphologically very similar to *M. granulata* (Müller 1905; see illustrations of Stager 1984). Kilham and Kilham (1975) showed by culturing auxospores and following subsequent growth that several varieties of *M. granulata* are size variants of a single taxonomic entity. More work of this kind would be useful in determining species boundaries within the genus.

No data are available on the nutritional requirements of *Melosira* species, so we must rely on distributional information to indicate possible resource needs. All the species of *Melosira* discussed here seem to have high growth requirements for silicon and would be poor competitors for this element. Kilham (1971b) and Kilham and Kilham (1975) argued on the basis of distributional data that *M. granulata* grows best where silicon is not limiting. Lund (1954) observed that the growth of *Melosira italica* is halted if Si falls below 10 μM . *Melosira* species should therefore be abundant in lakes in which silicon is nonlimiting during their periods of maximum growth. The situation for phosphorus is different. We suggest, based again only on distributional data, that the five species of *Melosira* can be ranked along a requirement gradient for phos-

phorus (Fig. 2): *M. distans* lower than *M. ambigua* or *M. agassizii*, which are lower than *M. granulata*, with *M. nyassensis* having the greatest growth requirement for phosphorus.

Melosira distans is a well known indicator of oligotrophic conditions (Hutchinson 1967). In Africa, it appeared in the Blue Nile (Sudan), along with *S. acus* and *Attheya zachariasi*, when phosphorus concentrations reached their lowest levels (Sinada and Abdel Karim 1984). It is also a large (24%) component of the diatoms in surface sediments from Lake Nyungu, Uganda (Gasse pers. comm.), along with *S. acus* and *S. ulna* (23%), both indicators of low P concentrations. This lake has very high Si levels and very low P concentrations (Melack 1978). We therefore hypothesize that *M. distans* has the lowest phosphorus requirements of the five species.

Huber-Pestalozzi (1942) characterized *M. ambigua* as occurring in lakes over a range of oligotrophic to eutrophic. In surface sediment samples from lakes Rugwero (Rwanda), Makat Ngorongoro (Tanzania), and Kivumba (Rwanda), *M. ambigua* comprises >20% of the diatoms and is associated with both *Synedra* species (low P requirements) and *M. granulata* (high P requirements). *Melosira ambigua* is abundant in the plankton of Lake Naivasha (again with *M. granulata* and *Synedra* spp.), especially during periods of increasing P limitation following a mixing event (Gasse et al. 1983; Kalf 1983). It is also abundant in nearshore areas of Lake Victoria (Lund 1954; Talling 1965; Richardson 1968). We therefore hypothesize that *M. ambigua* is intermediate between *M. distans* and *M. granulata* in its growth requirements for phosphorus.

Few data are available for *M. agassizii*, although it is prominent in Lake Victoria where it exhibits a narrow amplitude in abundance over the yearly cycle (Talling 1966). This species has also been reported in some surface sediment samples from other African lakes by Richardson (1968) and Gasse et al. (1983), where it usually co-occurs with *M. granulata*. We suggest that this species is, like *M. ambigua*, intermediate between *M. distans* and *M. granulata* in its phosphorus growth requirements. The po-

sition of *M. agassizii* relative to *M. ambigua* is equivocal at present.

Melosira granulata is the most widely distributed species of the genus in Africa. It is often reported in abundance in surface sediment samples (Kilham and Kilham 1975; Gasse et al. 1983), in cores (Fig. 1; Hecky and Haberyan in prep.), and in modern phytoplankton samples from lakes (Hecky and Kling 1986) and especially from rivers (Serruya and Pollinger 1983). *Melosira granulata* is a well known indicator of eutrophic conditions (Hutchinson 1967) and becomes abundant in the Laurentian Great Lakes under conditions of high phosphorus loading (Stoermer et al. 1981). We therefore hypothesize that *M. granulata* has a high growth requirement for phosphorus.

Melosira nyassensis is a large, heavy-bodied species that occurs predominantly in lakes Malawi and Victoria. The form in Lake Victoria is usually designated *M. nyassensis* var. *victoriae*. This species undergoes large-amplitude changes in abundance seasonally in Lake Victoria (Talling 1966) and reaches its peak densities in both lakes during the time of deepest mixing (Talling 1969). It is unlikely that nutrients are limiting at all during such periods; therefore we suggest that this species grows best under high phosphorus conditions.

One aspect of the ecology of *Melosira* species most often emphasized is the relationship between abundance and vertical mixing (turbulence). This genus is characterized by large filamentous forms, often heavy-bodied, which require some degree of mixing to keep them suspended in the water (Lund 1954). Titman and Kilham (1976) demonstrated that sinking rate in *M. agassizii* is high and dependent on the degree of nutrient limitation, with the highest sinking rates in phosphorus-depleted cells. During mixing events in lakes there will tend to be an inverse relationship between depth of mixing and light, and between light and phosphorus. We hypothesize that there is a tradeoff curve (Tilman et al. 1982) between light requirements and phosphorus requirements which distinguishes the *Melosira* species (Fig. 2). The species that has the highest light requirements and lowest P requirements for growth is *M. distans* and the

species with the lowest light requirements and highest P requirements are *M. granulata* and *M. nyassensis*, with *M. ambigua* and *M. agassizii* being intermediate.

Few data exist relating *Melosira* species to light regimes. In general, *M. distans* occurs under oligotrophic conditions where light levels can be quite high, and *M. granulata* often occurs in highly eutrophic lakes and turbid rivers where light is commonly very low and scattered. *Melosira ambigua* is intermediate between these two species. The other two species of *Melosira* are more likely related to light by the relationship that relates mixing depth (Z_m) to the depth of the euphotic zone (as measured by Secchi depth, Z_{SD} ; Z_m/Z_{SD} ; see Reynolds 1984). Both *M. agassizii* and *M. nyassensis* are heavy-bodied species that require turbulent conditions to deliver them to the euphotic zone. In Lake Victoria, *M. nyassensis* grows best during the period of maximum vertical mixing when the euphotic zone (1% of surface light) is approximately 14 m, with mixing to 60 m ($Z_m/Z_{SD} = 10$; we estimated Z_{SD} using data from Talling 1965 and the relationship between Secchi disk depth and the percentage of surface light determined by Beeton 1958); thus the population experiences light for only short periods on the average. In Lake Malawi, intense mixing to greater than 200 m can occur (Hecky and Kling 1986), with the population experiencing quite low light levels. Because *M. agassizii* can maintain populations throughout the year in Lake Victoria when the Z_m/Z_{SD} is lower (higher average light), we suggest that its light requirements are higher and P requirements lower than those of *M. nyassensis*.

One of us (P.K.) noted an interesting morphological correlate to the distribution of the *Melosira* species along the light axis. The species having higher growth requirements for light (*M. distans*, *M. ambigua*) have very small pores and the species growing better under lower light conditions have large, less numerous pores (*M. nyassensis*; see figures of Stager 1984). There may also be a relationship between light and pore size within a species, with large- and small-pored forms (referred to as α and γ status by taxonomists; see Hustedt 1930) being related to

the light conditions under which growth occurred. One might expect that within a lake the large-pored form would predominate during periods of very deep mixing, and the small-pored form would predominate under conditions of higher light in shallow water or during periods of less intense mixing. Stoermer et al. (1981) found a tendency for a shift from large- to small-pored forms of *Melosira islandica* in the Laurentian Great Lakes during the period of temperature increase in the spring. This is the period when light is increasing and Z_m/Z_{SD} is decreasing. Similarly, they noted a tendency toward higher proportions of *M. granulata* colonies with large-pored cells in highly eutrophied regions (which are low light regions). If this relationship between pore size and light levels (or mixing depth) holds up to scrutiny, then it might be possible to use fossil *Melosira* species as indicators of past mixing conditions, assuming that light transparency is relatively constant. If a shift occurred in a core from large- to small-pored forms of *M. granulata*, then one might interpret this as a change from shallow, eutrophic conditions to deeper, less eutrophic conditions (especially if a rise in *M. agassizii* or *M. ambigua* accompanied this shift in pore size). Similarly, a case in which *N. fonticola* (see below) co-occurred with *M. nyassensis* (Stager 1984; Lake Victoria) might indicate a period of very large fluctuations in climate, because the *Microcystis/N. fonticola* association is associated with calm, stable conditions and *M. nyassensis* is associated with very deep, intense mixing. Pore size and density of *Melosira* species might be useful as "paleophotometers" or "paleobathymeters." It is also worth examining this relationship between pore size and light levels in other species of diatoms (*Stephanodiscus* spp.?: Theriot and Stoermer 1984) that can grow over a range of light intensities (and mixing regimes).

Nitzschia fonticola

The ecology of *N. fonticola* is fairly well understood. Cholnoky (1968) characterized this species as an obligate nitrogen heterotroph because it obtains combined nitrogen solely from amino acids (it apparently does not use NO_3^- , and it may not use NH_4^+).

Cholnoky's observations are not well documented and should be repeated. However, they are consistent with Guillard's (1962) research on a marine species of *Nitzschia* and Moss's (1973) investigation of the organic sources of nutrition for a variety of freshwater algae. *Nitzschia fonticola* is the most important obligate nitrogen heterotroph found in the lakes of East Africa and is often common in fossil assemblages (Gasse et al. 1983). Other species which also may be indicators of nitrogen heterotrophy are *Nitzschia kützingiana*, *Nitzschia palea*, and *Nitzschia thermalis* (Schoeman 1973). On the basis of our interpretation of the diatom stratigraphy of Lake Victoria, Uganda (Stager 1984), *Fragilaria brevistriata* is another possible candidate for nitrogen heterotrophy.

A key feature of the ecology of *N. fonticola* is that it lives in and on colonies of *Microcystis aeruginosa* (Täuscher 1980; Ganf 1974), a non-nitrogen-fixing blue-green alga which Reynolds (1984) characterized as one of the most *K*-selected members of the freshwater phytoplankton. *Microcystis* is remarkably well adapted to warm, stable environments that are not strongly limited by nitrogen or phosphorus (Robarts and Zohary 1984). When stratification breaks down in environments favored by *Microcystis*, it is often replaced, at least temporarily, by species of *Melosira*. The sediments of lakes that are often unstratified (unstable) contain fossil assemblages dominated by *Melosira* or other species, while the sediments of lakes that are generally stratified (stable) contain fossil assemblages that are often dominated by *N. fonticola*. These lakes must of course have levels of resources appropriate for the growth of *Microcystis* (with *N. fonticola*) and *Melosira* species.

Little is known about the ecological association between *N. fonticola* and *Microcystis*, but it is likely that *N. fonticola* only becomes important in the plankton when it is associated with *Microcystis*. *Nitzschia fonticola* probably benefits from its association with *Microcystis* by reduced losses from sinking and grazing as well as having a source of organic nitrogen compounds. On the other hand, *Microcystis* commonly occurs without epiphytic diatom associates. It

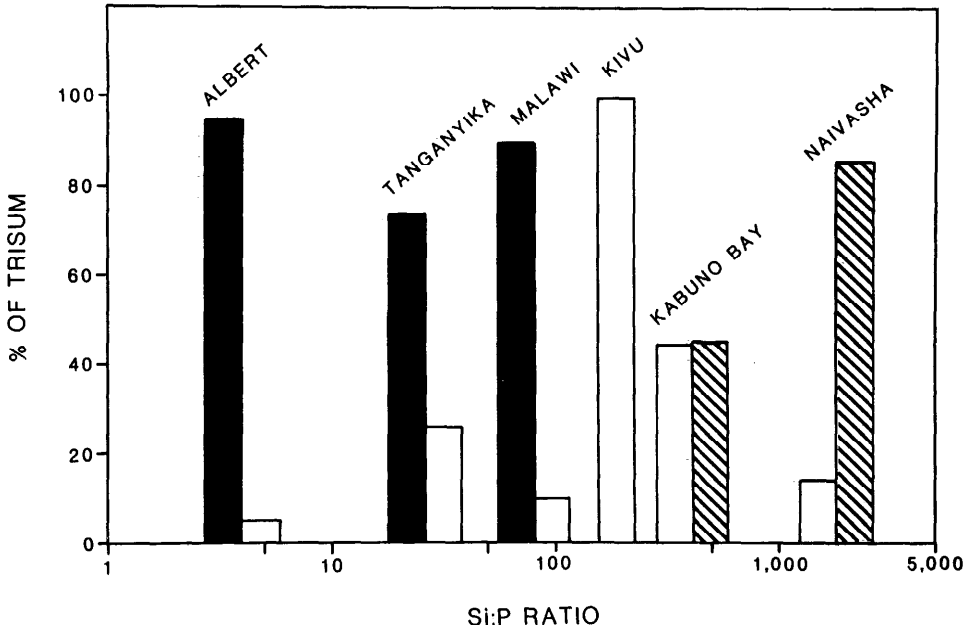


Fig. 3. Relative percentages of diagnostic surface sediment diatom microfossils in African lakes spanning a wide range of Si:P ratios. *Stephanodiscus* (black bars), *Nitzschia* (white bars; except *N. fonticola*, see text), and *Synedra* (hatched bars) species are given as a percentage of their trisum. Data are from the following sources: Lake Albert—Harvey 1976; Lake Malawi and Kabuno Bay—Hecky unpubl.; Lake Tanganyika and Lake Kivu—Hecky and Haberyan in prep.; Lake Naivasha—Richardson 1968. Si:P ratios for the lakes that are usually strongly stratified were calculated from nutrient concentration data for the submixing zone (the region directly below the mixed layer). These data were used because nutrients diffuse from the submixing zone into the mixed layer where they are utilized by planktonic diatoms. Lakes in this category and the sources used are: Lake Malawi—Hecky unpubl.; Lake Tanganyika—Coulter 1977; Lake Kivu and Kabuno Bay—Degens and Kulbicki 1973. Lake Albert and Lake Naivasha are well mixed, therefore we used concentration data for ambient nutrients from Talling (1963) and Melack (1976) to calculate Si:P ratios.

is widely accepted that algae generally liberate extracellular substances when they are nutrient limited (Hellebust 1974). Therefore, *N. fonticola* and the other algae often associated with *Microcystis* colonies (see Täuscher 1980; Hindák 1981) probably flourish only in nutrient-stressed populations of *Microcystis*. However, nutrients cannot be extremely limiting or *Microcystis* itself would be eliminated from the plankton. *Microcystis* has a fairly high growth requirement for phosphorus (Holm and Armstrong 1981), so it is usually abundant where phosphorus supply rates are relatively high. In light-limited populations of *Microcystis*, such as those studied by Robarts and Zohary (1984) at Hartbeespoort Dam (South Africa), nutrient limitation is apparently insignificant. Unfortunately, any co-occurrence with *N. fonticola* was not reported. In Lake Victoria (Uganda) where *N. fonticola*

(Stager 1984) and *Microcystis* (Talling 1966) presumably co-occur, nutrient limitation is suspected (Talling 1966). In Lake George (Uganda), nutrients and light are potentially limiting, and Ganf (1974) has observed *N. fonticola* to be associated with *Microcystis*. In sediment cores from Lake George, *N. fonticola* frustules are the dominant microfossils (Haworth 1977).

The available evidence suggests that the high abundance of *N. fonticola* in fossil diatom assemblages is an indicator of hydrodynamically stable conditions under which nutrient-stressed populations of *Microcystis* occur.

Conclusions

On the basis of the physiological mechanisms describing resource relationships among planktonic diatoms from temperate lakes, we have constructed two hypothe-

sized resource tradeoff curves for a number of species of planktonic diatoms that are abundant in African lakes. *Synedra*, *Nitzschia* (except *N. fonticola*), and *Stephanodiscus* species are suggested to compete along a Si:P resource ratio gradient. The modern African lakes exhibit a wide range of Si:P ratios and these diatoms appear to be distributed along this gradient as would be predicted from resource theory. *Stephanodiscus* and *Synedra* species predominate at the extremes of the gradient, while *Nitzschia* species predominate at intermediate Si:P values (Fig. 3). Although the modern lakes have a wide range of Si:P ratios and diatom assemblages, prior to 5000 B.P. *Stephanodiscus* species predominated over species in the other two genera in the same lakes (see Fig. 1). Prior to 10,000 B.P., *Stephanodiscus* predominated over all diatom genera. Much lower Si:P supply ratios must have existed in the past and diatoms were probably strongly Si limited until about 5000 B.P. The shift from strong Si limitation in all lakes toward P limitation in many lakes suggests a change in the availability of P and a tendency toward more oligotrophic conditions as the modern era was approached. Unfortunately the geochemical and limnological mechanisms governing phosphorus and silicon loading to tropical lakes are largely unknown and even informed speculation is unwarranted. However, we do know that the climate of Africa was comparatively moist between 12,000 and 3000 B.P. and that lake levels in many basins were high (Livingstone and Van der Hammen 1978). Between 6000 and 5000 B.P. lake levels had begun to fall in the Nainashasha Basin (Richardson and Richardson 1972) and *Stephanodiscus* was replaced by *Synedra* and *Nitzschia* species (other than *N. fonticola*).

The rigorous application of resource theory requires that these arguments be based at the species level (Tilman 1982; Tilman et al. 1982). We have lumped the planktonic forms of three genera and treated them as distinct groups along the Si:P tradeoff curve. It may be that there are a few species of *Synedra* and *Nitzschia* or of *Nitzschia* and *Stephanodiscus* that overlap in their resource requirements, but if species of *Synedra* and *Stephanodiscus* overlapped in Si

and P requirements we would take that as falsification of the hypothesis. Because of taxonomic uncertainties and the general paucity of species data linked with nutrient data, we have used the generic level for drawing distinctions among these diatoms.

We had expected to find that nitrogen or various metals might be important, but the only apparent relationships involving nitrogen are the nitrogen heterotrophy of *N. fonticola* (Cholnoky 1968) and perhaps the abundance of *S. berolinensis* under very low nitrogen conditions in Lake George (Ganf 1974). The resource ecology of these organisms is poorly understood, but diatoms may be extremely efficient at utilizing low concentrations of nitrogen. An adaptation of this type could have evolved in the ocean and been maintained as planktonic diatoms colonized freshwater environments (*but see* Round and Sims 1981). In any case, no clear pattern with respect to nitrogen emerged from the available distributional data.

Among the *Melosira* species we suggest a light:P tradeoff curve and we observe an apparent relationship between pore size and the light climate (a function of both turbidity and mixing depth) under which growth occurs. Species with small-pored forms are most abundant in high light conditions and those with large-pored forms are common under low light conditions. Environmental processes affecting variation in morphological characters of diatoms are an important area for future studies, especially because of the potential for more accurate descriptions of paleoenvironments.

The physiological ecology of African planktonic diatoms is completely unstudied. We have presented a series of testable hypotheses that appear to explain to some degree the distributions of a number of species important in African lakes. They have the potential to serve as sensitive indicators of climatic processes in the lake basins affecting supply rates of resources.

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