Green, bluegreen and diatom algae: Taxonomic differences in competitive ability for phosphorus, silicon and nitrogen

By David Tilman, Richard Kiesling, Robert Sterner, Susan S. Kilham and Frederick A. Johnson

With 2 figures and 1 table in the text

Abstract

Numerous laboratory resource-limited competition experiments performed on natural algal assemblages in continuous culture suggest that, of all the algal species in mid-latitude lakes, some species of diatoms are superior competitors for phosphorus, but that some species of green or bluegreen algae are superior competitors for nitrogen, and light. The Si:P and N:P ratios at which dominance shifted from one taxonomic group to another were temperature dependent, with diatoms dominant through a broader range of Si:P and N:P ratios at lower temperatures (less than ca. 14 °C) and green and bluegreen algae dominant at higher temperatures. Bluegreen algae dominated all N:P supply ratios (µM:µM) less than ca. 20 at 24 °C, but were not dominant at any N:P ratios at 17°C and 10 °C. These relationships support the hypothesis that temperature-dependent resource competition may be an important process structuring natural algal communities. They could explain the shift to dominance by bluegreen and green algae in mid-latitude, mildly-productive phosphorus-limited lakes with culturally derived phosphorus additions and warming.

Introduction

The majority of the mildly productive, mid-latitude lakes of North America are often said to have phosphorus limited phytoplankton because phosphorus additions lead to increase algal biomass (Hutchinson 1967; Schindler 1977; Schelske 1975; Stoermer et al. 1978) and because a strong correlation exists between phosphorus and algal standing crop (Vollenweider 1976; Dillon & Rigler 1974; Smith 1979). A recent re-examination of the available data has also shown a strong correlation between nitrogen levels and algal standing crop, especially in lakes with low nitrogen (N):phosphorus (P) ratios (Smith 1979), suggesting that nitrogen may be an important limiting resource for some phytoplankton species in some lakes. According to resource competition theory, different relative supply rates of two or more limiting resources should result in phytoplankton communities dominated by different species (Tilman 1977, 1982; Tilman et al. 1982). Whole-lake fertilization experiments have produced major changes in phytoplankton community composition,
with the pattern of dominance dependent on the pattern of fertilization (Schindler 1977; Kilham & Kilham 1984). Similarly, both the increased phosphorus loading rates associated with cultural eutrophication (Schelske 1975; Stömer et al. 1978; Vollenweider 1976) and the cessation of such phosphorus loading (Edmondson 1971; Edmondson & Lehman 1981; Schelske & Stömer 1972) have resulted in dramatic shifts in the relative dominance of the major algal taxonomic groups. Increased phosphorus supply, which shifts N:P and Silicon (Si):P supply ratios to lower values, is associated with a decline in the importance of diatoms while bluegreen and green algae increase in dominance. These shifts in relative dominance of the major types of phytoplankton are associated with changes in the standing crops and species composition of other trophic levels.

The dramatic and consistent shifts in the dominance of major algal groups suggest possible generalizations concerning the requirements of these taxa for limiting resources and the degree of similarity among species within a group. One hypothesis explaining these dominance shifts in phytoplankton is that the composition of natural algal communities at the species level is controlled by nutrient and light competition (Tilman 1977, 1982; Tilman et al. 1982; Kilham & Kilham 1984). Alternatively, it has been suggested that other processes, such as grazing (Porter 1973), sinking (Titman & Kilham 1976), allelopathy (Keithing 1978), and diseases control algal dominance patterns.

In this paper we report on a large series of continuous culture experiments with natural algal assemblages from which grazers and predators were removed. These experiments were designed to determine the direct effects of different relative resource limitations on phytoplankton community composition. Under these controlled conditions we were able to document the effects of several supply rates of limiting resources by experimentally manipulating N:P ratios, Si:P ratios, and temperature.

**Materials and methods**

Standard methods were used for all chemical analyses (Strickland & Parsons 1972), and all values (including ratios) are reported as micromolar (µM). Algal counts were performed microscopically using a Sedgwick-Rafter chamber. All algae were identified and counted at least to the level of genus. Biovolume for each species was calculated by approximate geometric shape.

Lake Superior algae were collected at 10 points along a transect from the mouth of the St. Louis River, Duluth, Minnesota, to a station 50 miles east by northeast in the western arm of Lake Superior. Along this natural gradient, Si:P ratios (µM of dissolved reactive Si to µM of soluble reactive P) ranged from 20 to 1500 and N:P ratios (NO$_3^-$ to soluble reactive P) ranged from 15 to 400. By mixing all the algal communities collected, we obtained an initial algal assemblage which should have included the superior P, N, and Si competitors for this range of environmental conditions. The Lake Superior assemblage included species in the following genera: Diatoms Asterionella, Diatoma, Fra-
gilaria, Stephanodiscus, Synedra, Rhizosolenia, Melosira, Cyclotella, Tabellaria; Chrysophytes: Chroomonas, Cryptomonas, Dinobryon, Ochromonas, Rhodomonas; Green algae: Pediasstrum, Saurastrum, Scenedesmus, Chlamydomonas, Microspora, Coelastrum, Golenkinia, Ankistrodesmus; Bluegreen algae: Anabaena, Lyngbya, Oscillatoria, Chroococcus; Dinoflagellates: Ceratium. Although they dominate much of the offshore area of this lake, Chrysophytes and Cryptofytes are much less common than diatoms in the western arm of Lake Superior (Munawar & Munawar 1978).

Eau Galle Reservoir, Wisconsin, algae were collected from surface water in spring, 1980, and treated similarly. In 1980, Eau Galle Si:P ratios ranged seasonally from 39 to 300 and N:P ratios ranged from 10 to 240. The inoculum included: Diatoms- Stephanodiscus, Nitzschia, Synedra, Asterionella; Chrysophytes- Chrysoeodes; Green Algae- Scenedesmus, Actinastrum, Tetraallanton; Bluegreen Algae- Oscillatoria, Aphanizomenon; Dinoflagellates- Ceratium.

Lake Michigan algae were collected offshore of Milwaukee, Wisconsin, with species representatives in the inoculum from the previously listed genera for Lake Superior.

The algal species in the assemblages were allowed to compete for resources in laboratory continuous cultures: well-mixed vessels with a constant input of fresh medium and a volumetrically equal output of culture medium and organisms. Our Lake Superior continuous cultures were 500 ml polycarbonate flasks containing 300 ml of medium, with a flow rate of 0.3 day \(^{-1}\). Eau Galle cultures were 250 ml polycarbonate flasks with a flow rate of 0.2 day \(^{-1}\). Lake Michigan cultures were 500 ml polycarbonate flasks with 400 ml of media with a flow rate of 0.25 day \(^{-1}\). Flow was maintained by Monostat peristaltic pumps, with sterile feeding media in polycarbonate reservoirs. Cultures were grown in Percival incubators, mixed at 180 orbits min \(^{-1}\) for 10s every min., and lighted by Cool White bulbs. Except for the light:P experiments, light was 300 μEin m \(^{-2}\) \(\text{day}^{-1}\) for the Lake Superior and Eau Galle experiments and 800 μEin m \(^{-2}\) \(\text{day}^{-1}\) for the Lake Michigan experiments. A 14:10h light:dark cycle was used throughout. The algal growth medium used was WC, modified as in Tilman (1981), with N, P and Si adjusted as needed. The Lake Michigan experiments were performed by S. S. K. in Woods Hole, Massachusetts, the Eau Galle experiments by F. A. J. in Minneapolis, and the Lake Superior experiments by D. T., R. K. and R. S. in Minneapolis. We report here the data from the steady state result of each continuous culture.

The resources supplied to each series of cultures established three different kinds of gradients. Along each gradient, there were two potentially limiting resources: silicon and phosphorus; light and phosphorus; or nitrogen and phosphorus. All resources other than the pair of limiting resources were supplied in excess for each of the gradients used. Each of the continuous cultures along a particular gradient received a specific ratio of the two limiting resources. The different supply points along the N:P, Si:P and light:P gradients correspond to different resource limitations.

The Lake Superior Si:P gradients (see Fig. 1) corresponded to the following Si and P concentrations (all in μM), respectively, in the influent medium of particular flasks: 184:0.59; 120:0.66; 85.9:0.80; 66.9:0.79; 53.6:0.92; 49.4:1.01; 39.8:1.57; 38.4:2.82; 31.4:6.04; 28.8:12.9; 27.2:28.6. Nitrate was supplied at 1000 μM. This gradient was replicated at 9°C and 15°C. Data reported here are from the last day, day 35. For the Lake Michigan experiments of January 1980, Si:P influent concentrations were 97.4:0.31 (2 cultures), 47.0:0.66; 46.0:10.0, and 4.45:4.89 (2 cultures). Nitrate was 1000 μM. Temperature was 10°C. Data are from day 46, the last day of the experiment. For the Eau Galle experiments, influent Si:P concentrations (μM) were 10:10 and 100:0.5. Nitrate was 200 μM. Data reported are from the last day, day 50.
Fig. 1. The relative proportion of diatoms, green, and bluegreen algae in continuous culture competition experiments was highly dependent on the ratio at which Si and P were supplied. At both 9°C and 15°C, diatoms were competitively dominant at high Si:P ratios, but were displaced at low Si:P ratios by green and bluegreen algae. These experiments used algal assemblages from Lake Superior.

For Lake Superior N:P experiments, concentrations supplied for October, 1980 were N:P: 30:15; 40:4; 60:2; 150:0.3; for July 1981: 20:10; 20:0.4; for July, 1982: 2:10, 2.5:5, 4:2, 3:3, 4:1, 10:0.5; 20:0.5; 20:0.2; 200:0.2, with this gradient replicated at 9°C, 15°C and 24°C. Silicate was supplied at 150 μM for all these experiments. For the N:P experiments, the final day was day 55 in 1980, day 50 in 1981 and day 58 in 1982. An infection of three of the N:P flasks by a chitrid fungus led to a greatly reduced total algal biomass. Data from these flasks are not reported. These flasks were all part of the July, 1982 Lake Superior N:P experiments, specifically the flasks at 24°C with N:P of 2.5:5 and 20:0.2, and the 17°C flask with N:P of 2:10.

For light:P experiments, light intensity and P concentrations supplied were (light as μEin m⁻² s⁻¹ and P as μM): July, 1981 — 210:0.4; 120:0.4; 45:0.4. All these were at 15°C with 200 μM Si. Data reported are from day 50.
Green, bluegreen and diatom algae

Results

These experiments were designed to test the hypothesis that taxonomic similarity correlates with competitive ability for limiting resources. It has already been hypothesized that some species of bluegreen algae, because of their ability to fix atmospheric nitrogen, should be superior nitrogen competitors and come to dominate lakes where it is an important limiting nutrient (Schindler 1977). It has also been proposed that bluegreen algae become dominant because of superior competitive abilities at warmer temperatures (Hutchinson 1967). Our experiments were designed to determine the extent to which N:P ratios, Si:P ratios, and temperature influence the relative dominance of major taxonomic groups.

Si:P Experiments

In all of the Si:P experiments, diatoms were competitively dominant at high Si:P ratios, for which all taxa should be phosphorus limited. Fig. 1 shows the results of the Lake Superior Si:P experiments. Diatoms were dominant in the high Si:P flasks at both 9°C and 15°C, and declined in dominance at lower Si:P ratios. At 15°C, the transition from dominance by diatoms to dominance by green algae occurred between Si:P ratios of about 70 and 5, with green algae dominant at Si:P ratios less than 5. At 9°C, diatoms were dominant through a much broader ratio range, only starting to decline for Si:P ratios less than 5, but were still the dominant taxon at Si:P of 1. The experiments performed on the algae of the Eau Galle Reservoir, Wisconsin, revealed that diatoms dominated the high Si:P experiments, and were rare in the low Si:P experiments at both 8°C and 16°C (Table 1).

The similar Si:P supply ratios of the Lake Michigan experiments produced nearly identical results; the diatom percent dominance for Lake Michigan agrees with the result of the Lake Superior experiments (Fig. 1: 15°C).

N:P Experiments

In the N:P experiments performed on Lake Superior phytoplankton, diatoms dominated the flasks at high N:P ratios at all temperatures with bluegreen algae dominant at higher temperatures and lower N:P ratios (Fig. 2). Starting with the same inoculum, diatoms were dominant at the highest N:P ratios at all temperatures. At 24°C, bluegreen algae dominated N:P ratios lower than about 100. Green algae had a peak of abundance at N:P of approximately 20. The 17°C experiments were never dominated by bluegreen algae. Diatoms dominated all of the N:P ratios used while green algae had a trend suggestive of increasing dominance at low to intermediate N:P supply ratios. Diatoms dominated all N:P ratios used at 10°C as well, with bluegreen
algal community from Eau Galle Reservoir, Wisconsin

<table>
<thead>
<tr>
<th>Si:P ratio</th>
<th>1</th>
<th>200</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Diatoms by cell number at 8°C</td>
<td>8%</td>
<td>99%</td>
</tr>
<tr>
<td>% Diatoms by cell number at 16°C</td>
<td>4%</td>
<td>79%</td>
</tr>
</tbody>
</table>

B. Algal Community from Lake Michigan

<table>
<thead>
<tr>
<th>Si:P ratio</th>
<th>0.9</th>
<th>4.6</th>
<th>71</th>
<th>313</th>
</tr>
</thead>
<tbody>
<tr>
<td>% Diatoms by cell number at 10°C</td>
<td>1.5%</td>
<td>1.3%</td>
<td>94%</td>
<td>93%</td>
</tr>
</tbody>
</table>

C. Algal Community from Lake Superior

1. N:P ratio, October 1980, at 15°C

<table>
<thead>
<tr>
<th>2</th>
<th>10</th>
<th>30</th>
<th>500</th>
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<tbody>
<tr>
<td>% Diatoms (by biovolume)</td>
<td>0%</td>
<td>0%</td>
<td>94%</td>
</tr>
<tr>
<td>% Greens</td>
<td>100%</td>
<td>96%</td>
<td>0%</td>
</tr>
<tr>
<td>% Bluegreens</td>
<td>0%</td>
<td>4%</td>
<td>6%</td>
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<table>
<thead>
<tr>
<th>2</th>
<th>10</th>
<th>50</th>
</tr>
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<tbody>
<tr>
<td>% Diatoms (by biovolume)</td>
<td>20%</td>
<td>98%</td>
</tr>
<tr>
<td>% Greens</td>
<td>79%</td>
<td>1%</td>
</tr>
<tr>
<td>% Bluegreens</td>
<td>1%</td>
<td>1%</td>
</tr>
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3. Light:P ratio, July 1981, at 15°C

<table>
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<tr>
<th>200</th>
<th>300</th>
<th>525</th>
<th>1500</th>
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<tbody>
<tr>
<td>% Diatoms (by biovolume)</td>
<td>24%</td>
<td>97%</td>
<td>97%</td>
</tr>
<tr>
<td>% Greens</td>
<td>67%</td>
<td>3%</td>
<td>3%</td>
</tr>
<tr>
<td>% Bluegreens</td>
<td>9%</td>
<td>0%</td>
<td>0%</td>
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The light:P experiments (Table 1) showed diatom dominance at all but the lowest ratio, at which ratio green algae were dominant. Thus diatoms were dominant under conditions of P limitation but were displaced by green algae when light may have become limiting at 15°C.

Discussion

Results of our experiments revealed consistent responses of different algal communities. The first major pattern was the temperature dependence of dominance by bluegreen algae and diatoms. Bluegreen algae dominated a broad range of N:P ratios at 24°C, but were very rare in the experiments at these same ratios at 17°C and 10°C even though these experiments were started
Fig. 2. The effect of the supply ratio of N and P on the relative abundance of diatoms, green algae and bluegreen algae in continuous culture experiments on algal assemblages from Lake Superior. Experiments were performed at 10°C, 17°C and 24°C.

with the same inoculum and all inocula were gradually acclimated to the experimental temperatures. Viable bluegreen algae were observed in all of the flasks during the experiment, but they were rare at the lower temperatures.
Comparably, diatoms were dominant throughout the full range of N:P ratios at 10°C, less dominant at 15°C and 17°C, and dominant only at the highest N:P ratios at 24°C. Green algae tended to reach their peak dominance at intermediate N:P ratios at 17°C and 24°C, to dominate low N:P and low Si:P ratios at 15°C, but to be less dominant at 10°C. Thus, diatoms were most dominant at cooler temperatures, green algae at intermediate temperatures, and bluegreen algae at warmer temperatures under identical resource supply (Tilman & Klissling 1984).

At the species level, the temperature dependence of nutrient limited growth results in changed maximum growth rates and half-saturation constants (Tilman et al. 1981; Mechling & Kilham 1982; Thomas & Dooson 1974). These changes appear related to temperature specific physiological characteristics of cells such as cell quota (Rhee & Gotham 1981; Tilman et al. 1981; Li 1980). Competitive ability predicted by a Monod growth model for two diatoms illustrated a temperature dependent outcome of competition (Tilman et al. 1981), yet these two species had very similar ranges of half-saturation constants for Si. Coupled with our results, this suggests that algal species within a taxonomic group have similar optimal temperature ranges, and potentially competitively dominate these ranges. Alternatively, it may be that species which have different temperature optima than observed for their taxon did not occur in the lakes sampled.

The results also showed that these taxa differed in their competitive abilities for the various limiting resources. Diatoms dominated the higher N:P, Si:P, and light:P ratios at all temperatures. When such ratios are high, phosphorus should be limiting the growth of most of the algal species present. A high ratio (numerical value) means that the resource other than phosphorus (N, Si, or light) is in relative high supply. The decline in the dominance of diatoms and the increase in the abundance of other taxa at low N:P, Si:P, and light:P ratios suggests that all of the species of diatoms present were inferior competitors for N and light compared to some species in the other taxa. The transition from dominance by green algae to diatoms as Si:P ratios were increased (Fig. 1) is strong evidence that diatoms were superior competitors for phosphorus. Diatoms were increasingly dominant as phosphorus was increasingly limiting. Essentially identical results were obtained for the Lake Michigan and Eau Galle Reservoir algal assemblages, showing that the trends observed in Lake Superior may hold, in general, for north temperate algal communities for which Si and P are limiting. Recently reported work with Lake Constance algal assemblages (Sommer 1983) strongly supports the generality of these results.

Of all the freshwater algae included in a recent review (Tilman et al. 1982), Synedra filiformis had the lowest reported phosphorus requirement. Most of our whole-community continuous cultures have been dominated by one of
several species of *Synedra* at the highest resource:P ratios (see also Sommer 1983), suggesting that *Synedra* species are the best phosphorus competitors of the freshwater algae at the temperatures studied. Interestingly, *S. filiformis* also had one of the highest reported requirements for silicon, implying specialization in resource competitive ability (Tilman et al. 1982). The degree of specialization is also indicated by the separation of different diatom species along our Si:P gradients. There were marked and continuous changes in the species compositions of the cultures along the Si:P gradient of Fig. 1 and the N:P gradient of Fig. 2. For example, the distribution along the gradient of each of the major species could be roughly fit by a Gaussian curve, with *Chlamydomonas* at its peak relative dominance at lowest Si:P ratios, followed by *Fragilaria*, *Asterionella*, *Diatoma*, *Tabellaria*, and then *Synedra* at 9 °C, in Fig. 1. These results imply that the cost of increased competitive ability for one resource may be loss of competitive ability for another (see below).

The competitive displacement of diatoms by bluegreen algae at low N:P ratios at 24 °C implies that some species of bluegreen algae were the superior competitors for nitrogen at this temperature. Their displacement by diatoms at high N:P ratios, though, demonstrated that this was not just a temperature effect. The dominance by bluegreen algae is consistent with the hypothesis that they are superior nitrogen competitors because of their ability to fix atmospheric nitrogen. These results agree with Smrn’s (1983) data demonstrating that lakes dominated by bluegreen algae have N:P ratios less than ca. 60 ($\mu$M/$\mu$M). There was a separation of bluegreen algal species along the N:P gradient in these experiments, with *Anabaena flos-aquae* dominating at the lowest N:P ratios. Under these conditions it has numerous heterocystous cells and a colonial morphology. These results are consistent with the already proposed hypothesis that bluegreen algae may be superior competitors for nitrogen (Schindler 1977), but also suggest that they may be inferior competitors for phosphorus, compared to diatoms, at least for the range of temperatures we used.

Increased competitive ability for one resource seems to be associated with decreased competitive ability for other resources. If resource competition is an explanation for the coexistence of species in nature, theory requires “trade-offs” in the resource requirements of species (Tilman 1982). A species which is a superior competitor for one resource must be an inferior competitor for another. If such tradeoffs did not exist, a species could be a superior competitor for both resources, and dominate a broad range of environmental conditions. The dramatic decrease in dominance by diatoms as silicon becomes limiting suggests that diatom populations are constrained by their Si requirements. Diatoms also exhibit higher requirements for N and light relative to their P requirements (Tilman & Keesling 1984). If this specialization in nutrient requirements for growth did not occur, species of diatoms would be superior compe-
titors for a broad range of environmental conditions. In this sense, diatoms are incapable of dominating phytoplankton communities at all nutrient resource supply ratios.

Reported single-species growth physiologies of diatoms for Si and P suggest that an increased competitive ability for Si is accompanied by higher P requirements (Tilman et al., 1982). With this in mind, our results support the hypothesis that diatoms gain competitive ability for phosphorus, or specialize, by incurring a higher requirement for silicon and possibly other resources as well. As yet, no physiological basis or other proximate cause has been proposed to explain these constraints on competitive ability. The physiological mechanisms as well as the evolutionary implications of such tradeoffs, especially for patterns of speciation, deserve further study.

The consistency of the results of our experiments — performed in two different laboratories on the natural assemblages of algae from three different lakes — leads us to offer several hypotheses for future research: (1) Many diatom species are superior phosphorus competitors, but are inferior competitors for nitrogen and light compared to naturally co-occurring species of green and bluegreen algae, (2) Many bluegreen algal species are superior N competitors, but are inferior P competitors, (3) Diatoms, as a group, have their maximal resource competitive ability at low temperatures (less than about 15 °C), (4) Bluegreen algae have their maximal competitive ability at high temperatures (greater than about 20 °C). These hypotheses must be tested with detailed studies of the nutrient and temperature dependence of the growth physiologies of major species in these taxa.

Our results suggest that diatoms should dominate mid-latitude, mildly productive lakes when phosphorus is the major limiting resource, and that green and bluegreen algae should become dominant if nitrogen, silicon or light becomes limiting. This need not contradict the common seasonal decline in dominance by diatoms as phosphorus is depleted. The late summer dominance of many lakes by bluegreen algae may be caused by a combination of nutrient and temperature effects. Although P is very low at this time, N and Si are also very low. N:P ratios and Si:P ratios can be at their lowest. Additionally, surface water temperatures are at their seasonal high.

The consistency between the trends observed in these experiments and those observed in the phytoplankton of lakes (e.g. Smith 1983; Sommer 1983) suggests that resource competition and the temperature dependence of the competitive abilities of the major algal species are of major importance in controlling the species composition and algal dominance patterns in lakes. Our results also suggest that control of phosphorus loading rates and control of water temperature in the euphotic zone may be two important ways to influence the dominance of bluegreen algae in lakes, especially because these experiments showed that increased temperatures and decreased N:P, Si:P and Light:P...
ratios were associated with decreases in diatom dominance and increases in bluegreen algae.

**Summary**

Phytoplankton communities from Lake Superior, Lake Michigan, and Eau Galle Reservoir, Wisconsin, were subjected to a range of supply ratios of two potentially limiting resources. The resultant gradients in resource availability produced consistent results between the three independent research efforts. In all cases, diatoms were superior competitors under phosphorus limitation with green and bluegreen algae dominant under nitrogen limitation.

The dominance of these major taxa in relation to Si:P and N:P supply ratios was temperature dependent. Diatoms dominated a broader range of nutrient conditions below 14 °C. Green and bluegreen algae were dominant in flasks with moderate to low Si:P and N:P supply rates. Both of these groups dominated a wider range of supply ratios at higher temperatures (17 °C and 24 °C).

These results suggest that resource competition and its temperature dependence are one of the important mechanisms influencing the species composition and dominance patterns of phytoplankton communities.

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**References**


Addresses of the authors:

DAVID TILMAN, RICHARD KIESLING, ROBERT STERNER, FREDERICK A. JOHNSON, Department of Ecology and Behavioral Biology, 318 Church St. S.E., University of Minnesota, Minneapolis MN 55455, USA.

SUSAN S. KILHAM, Division of Biological Sciences, The University of Michigan, Natural Science Building, Ann Arbor MI 48109—1048, USA.