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"On the dominance of filamentous cyanobacteria in shallow turbid lakes"

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on the dominance of filamentous cyanobacteria in shallow turbid lakes

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abstract

The phytoplankton community of eutrophic shallow lakes is often dominated by filamentous cyanobacteria of the family *Oscillatoriaeae*. In this paper we follow two independent approaches to show that this situation is likely to be an alternative stable state of the algal community. First we analyze patterns of cyanobacterial dominance observed in the field, and show that these patterns imply that the algal community is a hysteretic system with two alternative equilibria. Then, we construct a simple competition model to show that hysteresis should in fact be expected from differences in physiology between cyanobacteria and algae. The basic mechanism is that cyanobacteria are the superior competitors under conditions of low light, but also promote such conditions as they can cause a higher turbidity per unit of phosphorus than other algae. This theory of hysteresis offers an explanation for the resistance of cyanobacteria dominance in shallow lakes to restoration efforts by means of nutrient reduction.

KEY PHRASES

Dominance by Cyanobacteria
Competition for Light
Hysteresis in Phytoplankton Communities

KEY WORDS

Oscillatoria
Cyanobacteria
Blue-green algae
Catastrophe
Alternative Stable States
Model
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introduction

Several physiologically distinct groups of cyanobacteria can be discerned, but in limnology especially the colony forming cyanobacteria like *Microcystis, Oscillatoria, Anabaena* and *Aphanizomenon* have received much attention because they often dominate the plankton in eutrophic lakes (e.g. Sas 1989; Trimbee and Prepas 1987; Smith 1986; Reynolds 1984; Schindler 1975; Berger 1975).

It has been argued that cyanobacteria are favoured by high pH and low CO_2 availability because of their low half-saturation constant for CO_2 uptake (Shapiro and Wright 1984; Talling 1976). In shallow lakes and ponds, however, chlorophytes rather than cyanobacteria are often found to dominate under highly productive conditions when pH values are high (Jensen et al. 1994; Jeppesen et al. 1990; DeNoyelles and O'Brian 1978). Probably, CO_2 limitation is rare in shallow lakes because of the relatively large input of this nutrient from the atmosphere as well as from the sediment (Jensen et al. 1994).

Under certain conditions some cyanobacteria (e.g. *Anabaena* and *Aphanizomenon*) form specialized cells (heterocysts) that can fix atmospheric nitrogen. A widely cited idea is that such blue-greens become dominant when the N:P ratio is low (Smith 1983; Schindler 1977). However, the correlation of cyanobacteria to this ratio may well be spurious, stemming from an increase in P rather than a decrease in the N:P ratio (Trimbee and Prepas 1987). In a thorough analysis of data from 210 Danish shallow lakes no relationship between abundance of heterocystous cyanobacteria and nitrogen availability has been found (Jensen et al. 1994).

In this paper we analyze the mechanisms behind the often observed dominance of the filamentous cyanobacteria of the *Oscillatoria* group in shallow lakes. The most important genera in this family are *Oscillatoria, Planktothrix, Lyngbya* and in saline lakes at lower latitudes *Spirulina*, but probably the most important bloom forming species in temperate shallow lakes is *Planktothrix agardhii* (formerly *Oscillatoria agardhii*). Lakes dominated by Oscillatoriaceae are typically very turbid, and when winters are not too cold the dominance can even persist throughout the year (Sas 1989; Berger 1975). Blue-green dominance is considered an important problem by water quality managers. Although the phenomenon is associated with eutrophication, attempts to restore the original phytoplankton community in shallow lakes by means of reduction of the nutrient loading are often unsuccessful (Sas 1989).

In the following sections, we first analyze field data and construct a graphical model on the basis of the observed patterns that explains the hysteresis and discontinuous responses to nutrient management. Subsequently, we present and analyze a simple mathematical model based on laboratory data, showing that the graphical model is well in line with the expectations based on our knowledge of the physiology of *Oscillatoria*. In the discussion we link our results to classical competition theory, and discuss the role of seasonality, herbivorous zooplankton and the recently reported effects of allelopathic substances from macrophytes on cyanobacteria.

patterns in the field

We analyzed data from 55 Dutch lakes shallower than 3 meter to check the relation between nutrients and light conditions and the abundance of *Oscillatoriaceae*. Data were averaged per lake over the period July-August for a given year. For most lakes information is available over several years, and the total data set encompasses 118 lake-years. Relative abundance of Oscillatoriaceae is expressed as percentage of the total algal biovolume. The vertical light extinction coefficient, E (m^{-1}), is estimated from Secchi depth, S (m), and the chlorophyll-a concentration, Chl ($\mu g\ l^{-1}$) using a regression model ($E = 0.79 + 0.016\ Chl + 0.46/S$) that has been shown to predict light attenuation in shallow lakes better than Secchi depth or algal biomass alone (Scheffer et al. in prep.). To describe the light climate experienced by algae the depth (Z) of the mixed layer needs to be taken into account. In shallow lakes, thermal stratification does not occur for long periods, and the mixed depth can therefore be considered equal to the (average) lake depth. In this paper we characterize shade as the product *EZ*. This measure is inversely proportional to the ratio of euphotic depth to mixed depth ($Z_{eu}/Z_{mix} \approx 4.5/EZ$) that is sometimes used to characterize the light climate experienced by algae (Reynolds 1984).

There is no significant relationship between the relative abundance of Oscillatoriaceae and the concentration of phosphorus in our data-set (Table 1). Also the total-N concentration and the total-N/total-P ratio are unrelated to the *Oscillatoriaceae* dominance (Table 1). Light conditions under water, however, are clearly related to the relative abundance of Oscillatoriaceae (Table 1, Fig. 1). The correlation with Secchi depth is significant, but an even stronger relation is found with the more sophisticated shade indicator *EZ*. High abundance of Oscillatoriaceae occurs predominantly under shady conditions (Fig. 1). This correlation of cyanobacterial blooms with low light levels is in line with the results of an analysis of 22 lakes worldwide by (1986) and with recent Danish findings for shallow lakes (Jensen et al. 1994). Analyzing semiquantitative data from a set of 178 lakes and quantitative data from 32 lakes, Jensen and co-workers found that in both sets correlation of dominance by (nonheterocystous) cyanobacteria to the $Z_{eu}:Z_{mix}$ ratio was more than twice as high as the correlation of dominance to the total phosphorus concentration. Note that the points in Figure 2 are not clustered around the (logistic) regression line. Instead, most points are found at very high or very low *Oscillatoria* abundance. This impression is confirmed by the frequency distribution of the relative abundance of Oscillatoriaceae (Fig. 2). In the majority of the cases these cyanobacteria are either a minor component of the phytoplankton community or strongly dominant. The regression line (Fig. 1) roughly characterizes an average *Oscillatoria* abundance at different shade levels. However, the pattern might be more appropriately described as a high and a low band of data points, with high points being more frequent at high shade levels. Oscillatoriaceae tend to be either scarce or dominant, and the probability of the latter rises steeply with shade.

It is commonly noted that *Oscillatoria* dominance is associated to eutrophication (Romo and Miracle 1994; Sas 1989; Berger 1975) and that these cyanobacteria can disappear again in response to a reduction of the nutrient loading (Mur et al. 1993; Sas 1989). The above results suggest that it is the low light level rather than the high nutrient availability per se that leads to dominance by Oscillatoriaceae in eutrophic situations. If this is indeed the main causal link between *Oscillatoria* dominance and eutrophication, disappearance of these cyanobacteria in response to a reduction of the nutrient concentration should occur at comparable shade levels rather than at comparable nutrient levels in different lakes. Indeed this pattern has been described for a couple of well studied *Oscillatoria* dominated lakes (Mur et al. 1993). Sharp drops in the percentage of cyanobacteria (*Planktothrix*) have occurred in the lakes Schlachtensee and Veluwemeer where phosphorus concentrations have gradually decreased due to a reduction in loading. In Veluwemeer, cyanobacteria disappeared at a considerably lower phosphorus level than in the approximately 3 times deeper Schachtensee (Fig. 3 upper panel). However, the light climate (expressed as the ratio $Z_{eu}:Z_{mix}$) at which the cyanobacteria collapsed was practically the same in both lakes.

The abrupt character of the changes in these lakes (Fig. 3) seems typical for the transition between *Oscillatoria* dominance and other algal assemblages (Sas 1989). Interestingly, remarkably abrupt switches have also been described for tropical lakes. Here the species involved is *Spirulina platensis*, another representative of the *Oscillatoria* family. Accurate data are scarce, but some of these lakes are actually known to switch back and forth repeatedly. (1980), who described these patterns, noted that the relatively stable states of the community between the switches persisted for more than ten generations, indicating that they represent disjunct equilibrium states.

Analysis of the Dutch data set in a slightly different way reveals another important pattern. Lakes where *Oscillatoriaceae* dominate tend to be shady compared to lakes of the same nutrient level where these algae are rare (Fig. 4). The difference is especially marked for lakes with a total-P concentration of less than 0.3 mg l^{-1} (Fig. 4 lower panel). This suggests that Oscillatoriaceae dominance is not only favoured by shady conditions, but also promotes such conditions. Obviously, this sounds like a chicken and egg problem and causality cannot be inferred from correlations alone. Other differences between lakes may simultaneously influence shade and cyanobacteria in such a way that the same pattern is produced. Therefore, it is informative to see that individual lakes that alternate between cyanobacterial dominance and another algal community tend to show the same pattern (Fig. 5). In Lake Ijsselmeer, for instance, filamentous cyanobacteria have been rare over the past 20 years. However, during the summers of 1976 and 1989 the summer algal community has been dominated entirely by *Planktothrix agardhii*. In both summers chlorophyll-a was exceptionally high. Another Dutch lake, Eemmeer, is usually dominated by *Planktothrix*. In 1991, however, the cyanobacterial density was low most of the summer. This coincided with a drop in Chlorophyll-a.

a graphical model based on the field data

The patterns in the field data suggest that shade promotes *Oscillatoria* dominance (Fig. 1 and 3), but that Oscillatoriaceae also promote shady conditions (Fig. 4 and 5). This would imply an interesting positive feedback in the development of blooms of Oscillatoriaceae. The consequences can be seen more clearly by setting up a simple *graphical model* (Fig. 6), based on the empirically derived patterns.

As argued, shade experienced by the algae depends on the (mixed) depth and the vertical light attenuation coefficient. In a given lake, however, depth is fixed and shade therefore depends only on the light attenuation coefficient

(E), termed 'turbidity' in the following. Normally turbidity will increase with the phosphorus level starting at a background value (E_b) and levelling off at high P concentrations when light becomes limiting (Fig. 6 lower curve). When cyanobacteria dominate, turbidity will be higher at the same nutrient concentration (cf. Fig. 4), thus a separate turbidity-nutrient relationship should apply to *Oscillatoria* dominated situations (Fig. 6 upper curve).

The field patterns further suggest that the probability that Oscillatoriaceae will dominate the community depends strongly on the shade level. Since many other factors may have an effect on the probability of cyanobacterial dominance, it would be surprising if the response to shade would be identical in all situations. The fact that there is not one unique critical shade level that separates *Oscillatoria* dominated states from other data points in Figure 2 will at least in part be attributable to differences in various factors between lakes and errors in estimating shade. The graphical model refers to the behaviour of one hypothetical lake. The simplest assumption in this case is that there is a single critical shade level, which because of the fixed depth translates into a critical turbidity, E_{crit}, above which cyanobacteria will become dominant (Fig. 6 horizontal line). Above this critical shade level Oscillatoriaceae will become dominant, at lower turbidities other algae will dominate. This implies that below the horizontal line the cyanobacterial turbidity-nutrient relation is irrelevant, whereas above the critical level the other turbidity-nutrient relation is irrelevant. Neglecting these irrelevant (dashed) parts, the two curves combine with the middle segment of the horizontal line to an s-shaped curve of steady states that is typical of so-called catastrophic systems. The figure suggests that at low total-P levels only the non-cyanobacterial state is possible, whereas at very high total-P levels only the cyanobacteria dominated state exists. However, over a range of intermediate nutrient levels ($P_1<P<P_2$) both states are possible. Here, the community will tend to settle in either of the two states depending on whether the turbidity in the initial state is above or below the critical value (E_{crit}).

This graphical model implies that the response to changes in the nutrient level should be discontinuous ("catastrophic") rather than smooth. When, starting from a low total-P level, the nutrient loading of the lake is slowly increased, turbidity will gradually increase too. This smooth response ends when the critical total-P value (P_2) is reached, since above this level only the blue-green dominated state exists. When this "breakpoint" is passed the system will jump to a higher turbidity at the *Oscillatoria* dominated upper branch of the diagram. If from this point the total-P concentration is gradually reduced, the algal community will stay on the cyanobacteria dominated branch until the lower critical nutrient concentration (P_1) is reached, and then jump back to the lower branch. It can also be inferred that *Oscillatoria* will not easily disappear from lakes that have a high background turbidity (E_b).

a model of competition for light and nutrients

The above reasoning is based solely on the patterns observed in the field. In this and the next paragraph we construct a competition model and use it to analyze a completely independent set of information, namely the physiological characteristics of algae that can be measured in the laboratory. Instead of analyzing competition between many species as it occurs in the field, we simplify the problem by considering only one typical blue-green (b) and one typical green (g) algal species. For parameterization we use data from experiments with *Planktothrix agardhii* and *Scenedesmus protuberans* as examples of the two respective groups.

To build up the growth equations we assume the productivity of the algae to depend on the availability of nutrients and light. Losses due to mortality, respiration and flushing are subtracted from the gross productivity. For the dependence upon the nutrient concentration (n) we take the classical Monod form with a half-saturation concentration (h):

For simplicity we consider the total nutrient concentration in the system (P) to

$$\frac{n}{n + h} \qquad (1)$$

be constant, and define it as the sum of free nutrients (n) and nutrients present in blue-green (b) and green (g) algae:

$$n = P - g - b \qquad (2)$$

The dependence of productivity upon the underwater light climate is more difficult to write in a simple form. Obviously, light intensity varies in the course of the day and decreases also with depth. For an idealized well mixed system of homogeneous depth, the integration of photosynthesis over the light gradient can be treated elegantly (Huisman and Weissing 1994). However, in real lakes the situation is always much more complex. Since it is, nonetheless, obvious that available light and therefore relative productivity in the lake declines with turbidity, we directly describe this in a simple pragmatic light limitation function:

$$\frac{1}{1 + q\,E} \qquad (3)$$

where q is the sensitivity to turbidity and E is the Lambert-Beer light extinction coefficient. This coefficient depends on algal biomass as well as on other components of the seston such as resuspended sediment particles. For our minimal model we omit background turbidity and write E simply as a function of the density of algae and their specific extinction coefficients (k_g and k_b):

$$E = k_g g + k_b b \qquad (4)$$

Note that the sensitivity coefficient (q) is not solely dependent on the physiology of the algae, as it will decrease with incoming irradiation and increase with the mixed depth of the lake. Assuming the effect of nutrient limitation and light limitation to be multiplicative the complete model becomes:

$$\frac{dg}{dt} = g \left[r_g \frac{1}{1 + q_g (k_g g + k_b b)} \frac{P - b - g}{h + P - b - g} - d_g - f \right] \qquad (5a)$$

$$\frac{db}{dt} = b \left[r_b \frac{1}{1 + q_b (k_g g + k_b b)} \frac{P - b - g}{h + P - b - g} - d_b - f \right] \qquad (5b)$$

where d_g and d_b are the typical rates of losses due to respiration, sinking and mortality of both groups, and f is an extra species independent loss rate due to flushing of the lake. The incoming water is assumed to be free of algae and have a nutrient concentration equal to P in order not to affect our mass balance.

The dimensions of the parameter and the default values used to produce the figures that follow are listed in Table 2. The points we make in our formal model analysis, however, depend only on inequalities of pairs of parameters, not on the specific values that we assigned to produce the figures. All qualitative results follow from the assumption that blue-green algae have a lower maximum productivity (r), loss rate (d), and sensitivity to turbidity (q), but cause a higher turbidity per unit of nutrients (k) than other algae.
Thus the four basic inequalities are:

$$r_b < r_g \qquad d_b < d_g \qquad q_b < q_g \qquad k_b > k_g \qquad (6)$$

model analysis and results

To analyze the behavior of the model we first write it in a compact form:

$$\frac{dg}{dt} = g\ G\ (g,\ b,\ f,\ P) \tag{7a}$$

$$\frac{db}{dt} = b\ B\ (g,\ b,\ f,\ P) \tag{7b}$$

where the functions G and B are the ones presented in eqs. (5a) and (5b), respectively.

Like all competition models, our model (5) has three trivial equilibria:

. absence of both species (g=0; b=0)

. absence of blue-green algae ($g=g^{*}>0$; b=0)

. absence of green algae (g=0; $b=b^{*}>0$)

The values of g^{*} and b^{*} can be computed by solving the equations:

$$G\ (g,\ 0,\ f,\ P)=0 \qquad B(0,\ b,\ f,\ P)=0$$

with respect to g and b.

Since G and B are decreasing functions of g, b, and f and increasing functions of P, it follows from the implicit function theorem that g^{*} and b^{*} are increasing with P and decreasing with f, as one should expect.

For suitable values of the control parameters (f, P) the model can also have a non trivial (i.e. strictly positive) equilibrium (g^{+}, b^{+}) that can be obtained by solving the equations

$$G\ (g,\ b,\ f,\ P)\ =\ 0 \tag{8a}$$

$$B\ (g,\ b,\ f,\ P)\ =\ 0 \tag{8b}$$

with respect to g and b. This equilibrium corresponds to coexistence of both groups. It can be formally proven that such a coexistence is always unstable, and that the corresponding equilibrium (g^{+}, b^{+}) is a saddle for all parameter values satisfying inequalities (6).

The results can be illustrated by three state portraits (Fig. 7). These graphs summarize the model properties by showing the trajectories of simulations starting from many different initial states. Figures 9a and 9c correspond to situations where the same species wins the competition irrespective of the initial conditions, while figure 9b illustrates the situation in which both trivial equilibria ($(g^*,0)$ and $(b^*,0)$) are stable. In this case, the boundary of their basins of attraction is the stable manifold of the saddle. This is the dashed trajectory connecting the origin with (g^+, b^+). Simulations end in either of the trivial "monoculture" equilibria depending on which side of this boundary they start.

The next step is to explore how the mode of behaviour (i.e. state portrait) depends on the total-P level and the flush rate. Let us assume that for a given pair (f, P) both monoculture equilibria are stable (Fig. 7b). If departing from this situation we slightly perturb the parameters, the equilibria of the system will change. However, when the perturbation is sufficiently small the two equilibria will remain on the axis and, by continuity, the saddle (g^+, b^+) will remain in the positive quadrant. Consequently, the trajectories of the system will be perturbed, but qualitatively the state portrait remains the same. For a change of the qualitative properties of this system it is necessary that the saddle (g^+, b^+) disappears from the positive quadrant, which can only happen through a collision with one of the monoculture equilibria. This occurs when $(g^+,b^+)=(g^*,0)$, i.e. when the two equations:

$$G\ (g,\ 0,\ f,\ P)\ =\ 0 \qquad\qquad B\ (g,\ 0,\ f,\ P)\ =\ 0 \qquad\qquad (9)$$

have a solution with $g>0$, or when $(g^+,b^+) = (0,b^*)$, i.e. when the two equations:

$$G\ (0,\ b,\ f,\ P)\ =\ 0 \qquad\qquad B\ (0,\ b,\ f,\ P)\ =\ 0 \qquad\qquad (10)$$

have a solution with $b>0$. The equations (9) with $g>0$ implicitly define a curve, called a bifurcation curve, in the parameter space (f, P). On one side of this curve we have systems with only the non-cyanobacterial monoculture equilibrium (Fig. 6a), while on the other side of the curve both monocultures are stable (Fig. 6b). Similarly, the equations (10) with ($b>0$) define another bifurcation curve. This curve separates situations with two alternative stable states (Fig 9b) from those in which only the cyanobacterial monoculture is stable (Fig 9c).

The two bifurcation curves can be obtained by means of any computer package suitable for drawing implicitly defined curves. The result is shown in Fig. 8 where the labels [*g*], [*g/b*], [*b*] identify which equilibria are stable. The qualitative response of the system to changes in total-P concentration and the flush rate can be seen from this bifurcation graph. Starting in the region [*b*] where a cyanobacterial monoculture is the only stable state, a shift to the alternative state will only occur after the lower bifurcation line is passed. On the other hand, starting from the region [*g*] where the cyanobacterial monoculture is unstable, a switch to cyanobacteria will only occur after the upper bifurcation line is crossed. In the region [*g/b*] where two alternative equilibrium states are stable, the system will stay in its current equilibrium state, unless perturbations bring it within the basin of attraction of the alternative state. Note that beyond a flush rate of approximately 18% of the lake volume per day, cyanobacteria are predicted to be absent irrespective of the nutrient level. This fits well with the observation of Danish workers that large cyanobacteria are not found in lakes with a hydraulic residence time of less than 5 days (Erik Jeppessen, pers. comm.).

An alternative and more classical way of looking at the problem is to show the dependency of the systems equilibria upon the control parameters. Figure 11 shows how the extinction E in equilibrium (in fact a linear combination of g and b) varies with the total-P concentration and the flush rate. Note that Figure 11a represents a vertical and Figure 11b a horizontal cross-section of the bifurcation graph (Fig 10). The values P_1 and P_2 in the first hysteresis and f_1 and f_2 in the second hysteresis correspond to the intersections with the two bifurcation curves. It can be seen from those diagrams that a transition from blue-green to green dominance is always associated with a conspicuous drop in turbidity, and that in the vicinity of the breakpoints a small variation of a control parameter can be sufficient to induce the transition. Note that the hysteresis with respect to P corresponds well to the graphical model derived from the field data (Fig. 6).

The figures also show that although the upper branch of the hysteresis is entirely above the lower branch, extinction associated to cyanobacterial dominance is not always greater than that associated to green algae dominance. For example, Fig. 9a (f=0.1) shows that for $P=P_l$ the extinction E_b associated with cyanobacterial dominance is approximately equal to 1, while Fig. 9b (P=0.3) shows that for $f> f_l$ the extinction E_g associated to green algae dominance is greater than that. This supports the idea that in analysis of data from different lakes (cf Fig. 1) it is unlikely to find one critical shade level that separates cyanobacterial dominance from other states, because the critical level can depend on other factors, such as flushing, that affect the competitive balance.

discussion

In the first part of this paper we show that the presence of hysteresis in the algal community can be inferred from the patterns observed in the field. In the second part we use a mathematical model to show that competition between Oscillatoriaceae and other algae is a plausible explanation for this hysteresis in view of their physiological characteristics measured in the laboratory. The model results are robust in the sense that they require only qualitative inequalities between the two groups and do not depend on specific parameter values. It is reassuring to note that these inequalities are comparable to the requirements for hysteresis in other simple models.

As argued, hysteresis occurs if the non-trivial equilibrium is unstable. This "unstable coexistence" case is also one of the qualitative possibilities in standard Volterra competition models. In such models the mechanisms of competition are not specified. Instead, the intensity of inter- and intra-specific competition is defined directly. Unstable coexistence occurs in Volterra models if inter-specific competition is stronger than intra-specific competition. Indeed, in our case green algae have a competitive advantage in an environment dominated by green algae because there is more light in that situation, whereas cyanobacteria have an advantage in the turbid condition caused by their own dominance.

Our general result is also analogous to that obtained from the graphical models of competition for two resources elaborated by Tilman (Tilman 1985; Tilman 1982; Tilman 1977; Taylor and Williams 1975). Tilman's resource-ratio theory predicts that the coexistence between two competing species is unstable if each species consumes relatively more of the resource of which it also tolerates the lowest levels. In our case competition is for light and nutrients. Blue-greens cause a higher turbidity at the same nutrient level. In resource-ratio terms, this means that they use relatively more light. Since they are also the most shade tolerant group, this fits with the resource-ratio requirement for unstable coexistence.

Clearly, the model is a minimal model, i.e. it does not cover all possibly important mechanisms. Many other factors than the ones included in the minimal model will operate in real lakes. Some may enhance the hysteresis, while others will tend to promote coexistence instead.

A mechanism that has been suggested before to explain the absence of filamentous blue-greens in relatively clear water is the fact that their photosynthesis is reduced at high light intensities (Van Liere and Walsby 1982). Photo-inhibition, which is not included in the model, will tend to enhance hysteresis, as it emphasizes the competitive inferiority of blue-greens in situations of low turbidity. In extreme cases hysteresis could even arise from it in the absence of any competing species (Toha et al. 1981), as the net growth of blue-greens in shallow clear water may be negative due to too high light intensities.

Another topic of much discussion with respect to cyanobacteria is their inedibility. Even large herbivorous zooplankters are unable to effectively consume filamentous cyanobacteria under most conditions (Gliwicz and

Lampert 1990; Schindler 1971; Arnold 1971). Viewed in more detail the interaction of filamentous cyanobacteria herbivorous zooplankton and edible algae is rather intricate, but an obvious implication of the inedibility is that grazing mortality will in general be lower for filamentous blue-greens than for edible algae. It can be inferred from the model results that this difference will tend to make the hysteresis more pronounced, as it enhances the already existing difference in (non-grazing related) loss rates ($d_b < d_g$) that is one of the four basic inequalities (Eq. 6) causing the hysteresis.

Although photoinhibition and inedibility should thus promote the expected hysteresis further, an absolute monoculture of filamentous blue-greens as predicted by the minimal model is never observed in real lakes (Fig. 2). Obviously, the monoculture prediction is an artefact of simplification. Many studies have shown that spatial heterogeneity and temporal variation of the environment help to prevent competitive exclusion and it seems reasonable to assume that both factors play a role in algal communities as well.

In large lakes, depth as well as concentrations of suspended solids, nutrients and algae can show a considerable horizontal variation. In such cases, it may well be that the competitive balance is in favour of blue-greens in only part of the lake. A simple thought experiment suffices to show that this may promote coexistence. Imagine a lake with distinct shallow and deep regions. Suppose that in case of complete isolation of the regions cyanobacteria can dominate in the deeper parts while losing the competition in the shallow regions. Now consider a continuous slight mixing causing a very small input of the competitive inferior group in each part. Because of the stability of both equilibria such minor changes are not sufficient to destroy the dominance of the other group. However, the continuous mixing will prevent competitive exclusion and cause coexistence in all regions. Very strong mixing between the parts will cause the system to be homogeneous again, and cause cyanobacteria to be either dominant or absent from the whole lake. It can thus be inferred that coexistence should be favoured in spatially heterogeneous lakes or interconnected sets of lakes where horizontal mixing is not too strong.

It has been demonstrated that temporal variation of the environment is another important process preventing competitive exclusion in algal communities (e.g. Padisak et al. 1993) . This surely applies to *Oscillatoria* dynamics. Although these algae can stay dominant throughout the year in eutrophic lakes (Sas 1989) the seasonal pattern depends on the temperature conditions. In Denmark overwintering of filamentous blue-greens occurs hardly at all (Jeppesen, pers comm.), while in the milder climate of The Netherlands, the dominant *Planktothrix agardhii* disappears from the eutrophic shallow lakes only in cold winters (Berger 1975). Winter can apparently bring the system past the breakpoint below which blue-green dominance ends. The sensitivity of *Planktothrix agardhii* to cold winters fits with the observation that the growth of this species like that of most large algae drops relatively steeply with temperature (Reynolds 1988). Obviously, seasonal alternation between blue-greens and other algae implies 'coexistence' during the transitional phase, and especially averages over a period including a transition will suggest coexistence.

Although the field patterns as well as the model results indicate that nutrients, through their effect on shade, influence the competition between *Oscillatoriaceae* and other algae, it is clear that temperature and flush rate are also important for the competitive balance. Recent studies have pointed out a fourth potentially important factor that may affect cyanobacterial dominance. Various aquatic macrophytes have been shown to release substances that inhibit the growth of cyanobacteria while having a much smaller impact on the development of other algae (Jasser 1995; Gross and Sütfeld 1994), and bag experiments in the field demonstrated that plants tend to cause a switch from cyanobacterial dominance to a dominance by green algae even though total algal biomass is not significantly affected (Jasser 1995).

The current information is insufficient to see exactly how the effects of nutrients (shade), flush rate, temperature and allelopathic substances on the competition interact. In general, however, a catastophic system will show hysteresis in its response to all control variables. Also the 'threshold value' for one variable will normally depend on the value of the other variables. The latter is illustrated for the combination of flushing and nutrients by the model analysis (Figs. 10 and 11). At low nutrient levels, the sensitivity to flushing increases. An example of the combined effects of nutrients and temperature is provided by the history of eutrophication of lake Albufera in Spain (Romo and Miracle 1994). In the 1970's eutrophication had caused the phytoplankton community to be dominated by Oscillatoriaceae in summer and autumn, but in the spring chlorophytes and diatoms were still dominant. Ongoing enrichment in the 1980's, however, led the chlorophyll levels to increase further, and *Oscillatoria* became dominant throughout the season, suggesting that the cyanobacterial dominance is less sensitive to the low temperatures when nutrient levels are higher.

In conclusion, field patterns as well as our physiology based model indicate that dominance by Oscillatoriaceae can be an alternative stable state of the algal community of shallow lakes because these shade tolerant cyanobacteria are able to cause an increase in turbidity that favours their competitive advantage. The relative inedibility of filaments to zooplankton may further enhance the stability of blue-green dominance. The model and field observations indicate that high flush rates reduce the probability of blue-green dominance because of their relatively slow growth rates. In addition, there is evidence that low winter temperatures and allelopathic substances from aquatic macrophytes can affect the competitive balance in favour of other algae.

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TABLE 1

Significance of the relation between relative abundance of Oscillatoriaceae expressed as a fraction of the total algal biovolume and various environmental factors. P_r denotes the significance of the regression coefficient of a sigmoidal logistic regression model through the data (e.g. the regression line in Fig. 1). P_c denotes the significance of the Spearman rank correlation.

	P_r	P_c	n
shade (*EZ*)	0.001	0.00001	118
Secchi	0.092	0.0015	118
mean depth	0.55	0.91	118
Total-P	0.38	0.45	118
Total-N	0.79	0.11	103
Total-N/Total-P	0.64	0.69	103

TABLE 2

Parameter dimensions and the values used to produce the figures. *Scenedesmus protuberans*, and *Planktothrix agardhii* served as typical examples of green algae (*g*) and filamentous blue-greens (*b*). The sources used to estimate the parameter values are: *(I)* (1977b); *(II)* (1979); *(III)* (1984); *(IV)* based on a *k*-value of 0.1 $m^2\ g^{-1}$ cell-biomass (Kirk 1983) and P-concentrations in phytoplankton compiled in Table 15 of (1984); *(V)* estimated using equation (5) for a temperate lake with a depth of 3 m from a lab experiment by (Mur et al. 1977b; Mur et al. 1977b) in mixed water columns with varying turbidity.

	g	*b*	dimensions	sources
r	1.2	0.6	day^{-1}	(I)
d	0.12	0.06	day^{-1}	(II)
h	0.003	0.003	$mg\ P\ l^{-1}$	(III)
k	5	10	$m^2\ g\ P^{-1}$	(IV)
q	2	1	m	(V)

FIGURES

Fig. 1 Relative abundance (% biovolume) of Oscillatoriaceae plotted against an index of under water shade experienced by the algae (the product of mean lake depth and the vertical light attenuation coefficient, *EZ*), for 55 shallow (mean depth < 3m) Dutch lakes averaged over the period July-August. For several lakes information from different years is included. The total data set encompasses 118 lake-years. The line represents a sigmoidal logistic regression model through the data (p of regression coefficient = 0.001, Table 1). The Spearman rank correlation coefficient of the data points is 0.40 (p = 0.00001).

Fig. 2 Frequency distribution of the relative abundance of Oscillatoriaceae (% of total algal biovolume) in the shallow lakes data-set described in the legend to Figure 1.

Fig. 3 The decline of cyanobacteria (dominated by ***Planktothrix agardhii***) with a reduction of the nutrient level in the Lakes Schachtensee (-----) and Veluwemeer (_____). The collapse of *Planktothrix* occurs at a higher total-P level in the shallower Lake Veluwemeer (upper panel), but both lakes switch at roughly the same underwater light conditions expressed as the ratio of euphotic depth to mixed depth, Z_{eu}/Z_{mix} (lower panel) (redrawn from (1993)).

Fig. 4 Under water shade (*EZ*, see legend Fig. 1) as a function of the total phosphorus concentration. Solid dots refer to lakes where Oscillatoriaceae comprise more than 50% of the algal biovolume open dots are for lakes with less than 50% Oscillatoriaceae. The upper panel represents the entire data-set described in the legend to figure 1. The lower panel represents the subset of lakes where the total phosphorus concentration is less than 0.3 mg l^{-1}. The regression lines are computed for the subset of data represented in the lower panel. The upper regression line is for the *Oscillatoria* dominated lakes (solid dots), the lower line for the other lakes.

Fig. 5 Average summer chlorophyll-a concentrations plotted against the total-P concentration in different years for two eutrophic shallow lakes. Blue-green dominated years are marked as solid dots. Chlorophyl is the main light attenuating seston component in these lakes, and shade will be higher in the years with higher chlorophyll levels.

Fig. 6 Generalized diagram of the equilibrium states of the algal community of shallow lakes inferred from the patterns observed in the field (see text for explanation).

Fig. 7 Sets of simulated trajectories illustrating the three possible state portraits of the model: [*g*] a monoculture of green algae is the only stable equilibrium; [*g/b*] initial conditions determine the final state; [*b*] a monoculture of blue-green algae is the only stable equilibrium.

Fig. 8 Bifurcation diagram of the model showing for which combinations of flush rate (f) and total-P concentration (P) blue-green algae [*b*] or other algae [*g*] will dominate, and for which combinations those states are alternative equilibria [*g/b*].

Fig. 9 Hysteresis shown as the response of the turbidity (E) with respect to the control parameters total-P (P) and flush rate (f).

Fig. 1

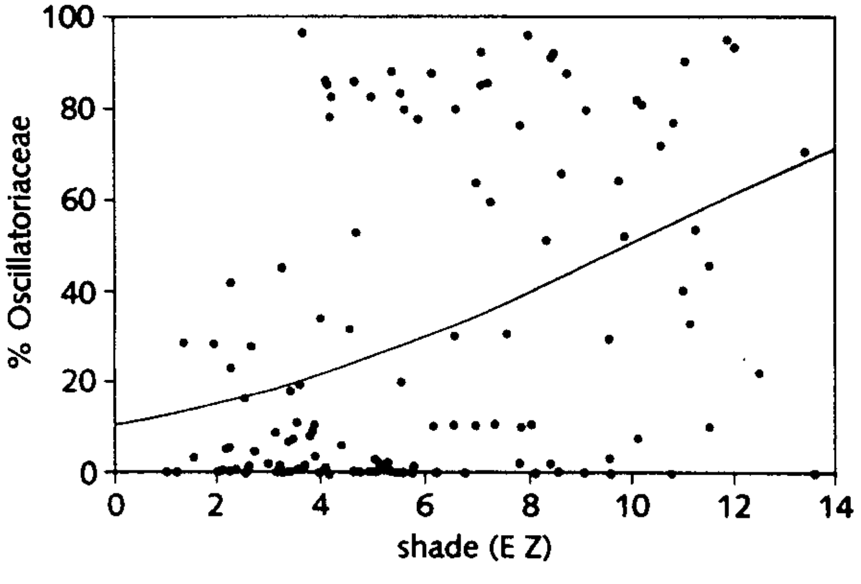


Fig. 2

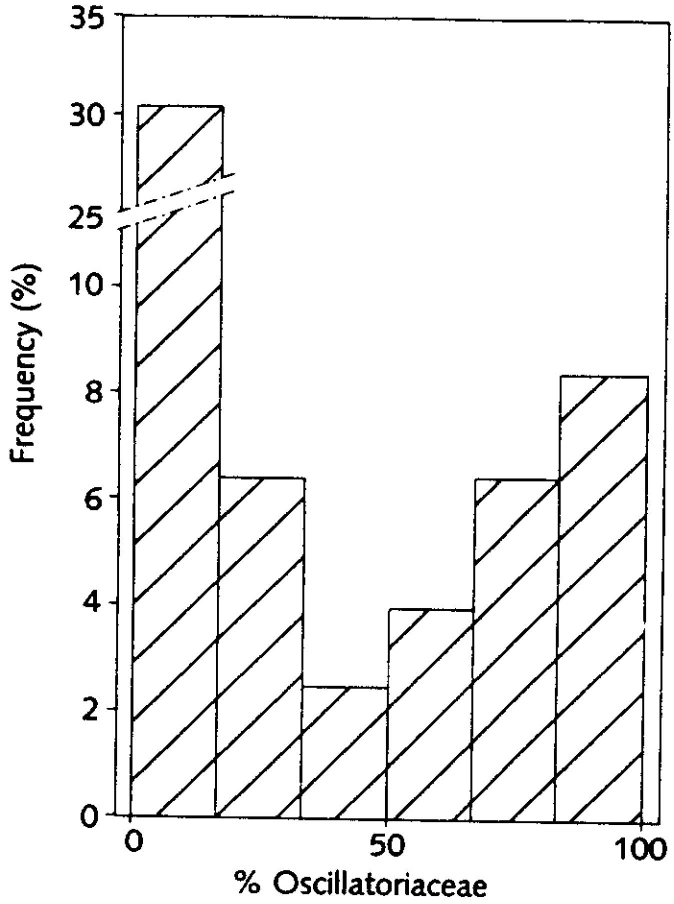
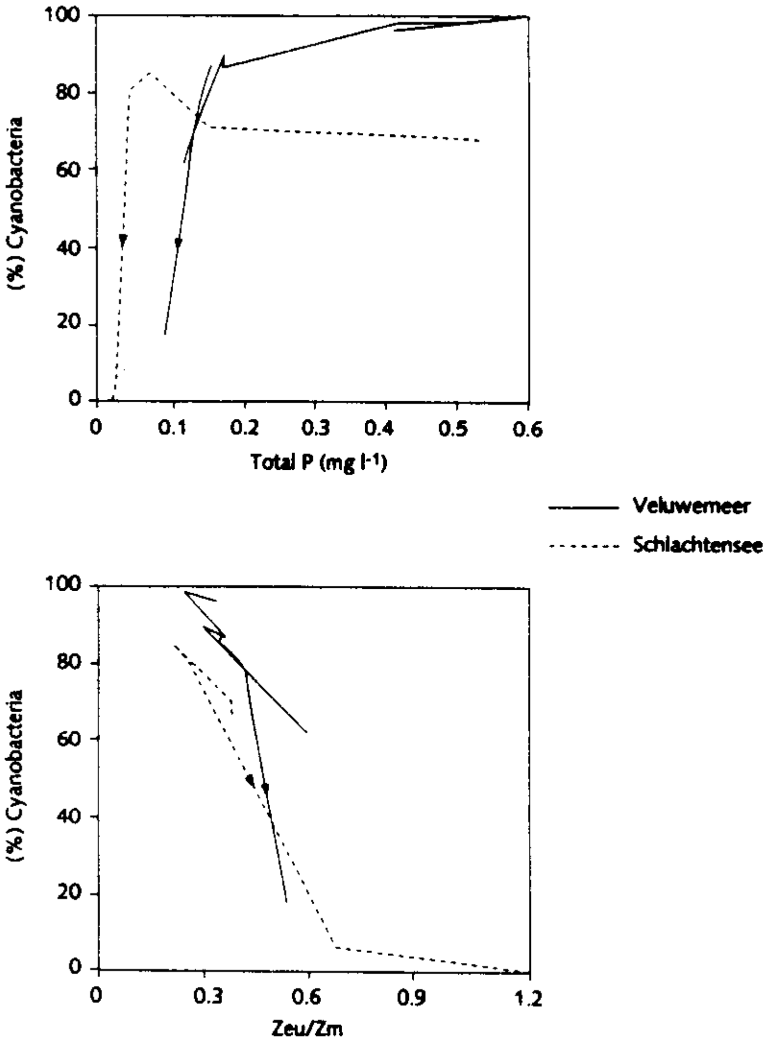
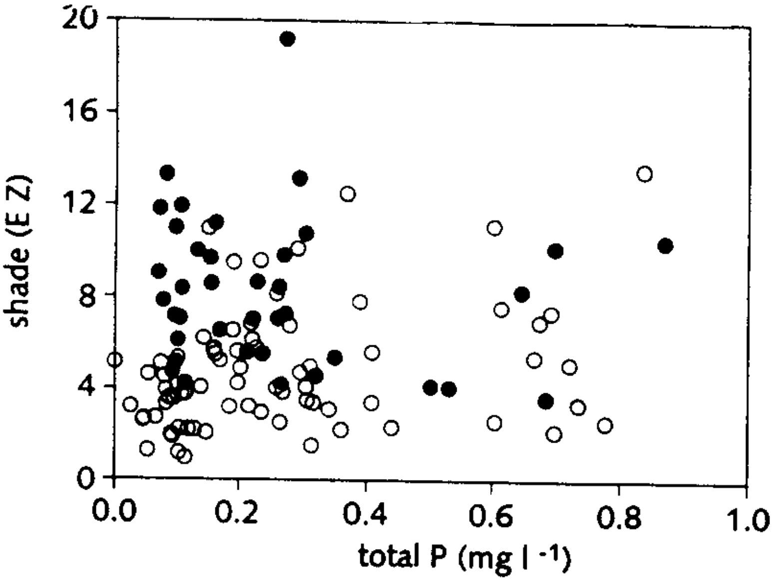


Fig. 3


100
80
60
40
20
0
(%) Cyanobacteria
0
0.1
0.2
0.3
0.4
0.5
0.6
Total P (mg l-1)
Veluwemeer
Schlachtensee
100
80
60
40
20
0
(%) Cyanobacteria
0
0.3
0.6
0.9
1.2
Zeu/Zm


shade (E Z)
0
4
8
12
16
20
0.0
0.2
0.4
0.6
0.8
1.0
total P (mg l -1)

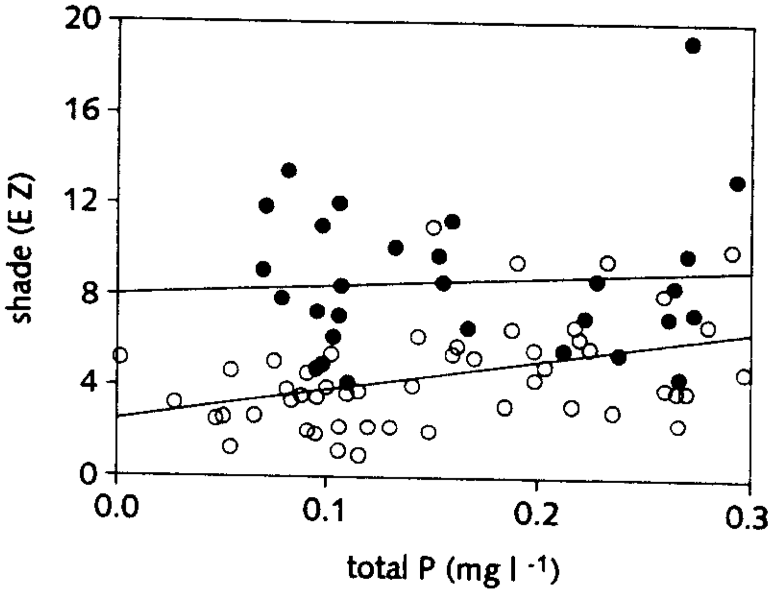
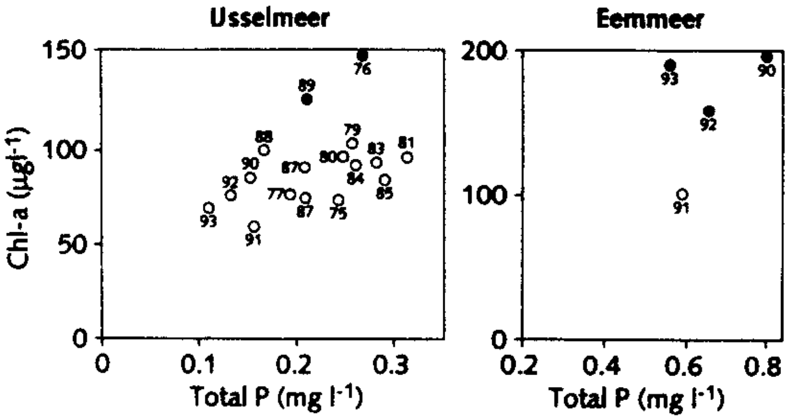

shade (E Z)
0
4
8
12
16
20
0.0
0.1
0.2
0.3
total P (mg l -1)

Fig. 5


Usselmeer
Eemmeer
Chl-a (µg l-1)
150
100
50
0
0
0.1
0.2
0.3
Total P (mg l-1)
76
89
79
88
83
81
90
87
80
84
92
77
85
93
87
75
91
200
100
0
0.2
0.4
0.6
0.8
Total P (mg l-1)
93
90
92
91

(a) *(b)*

Fig. 6

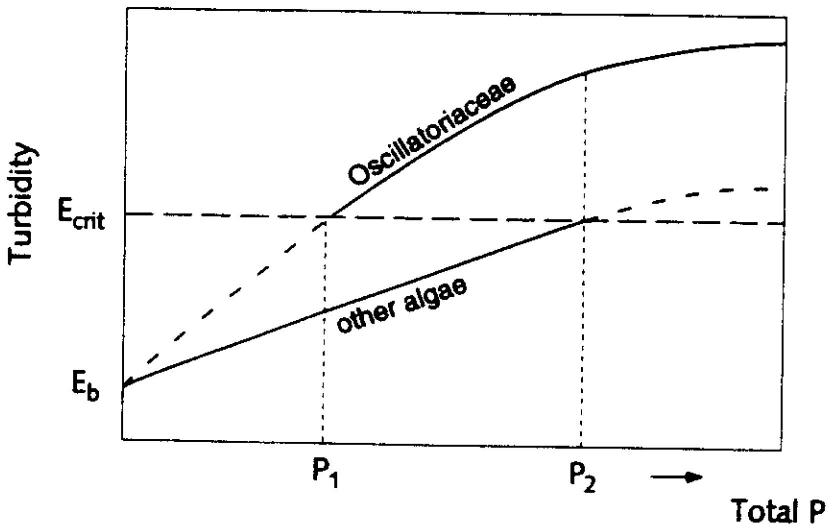
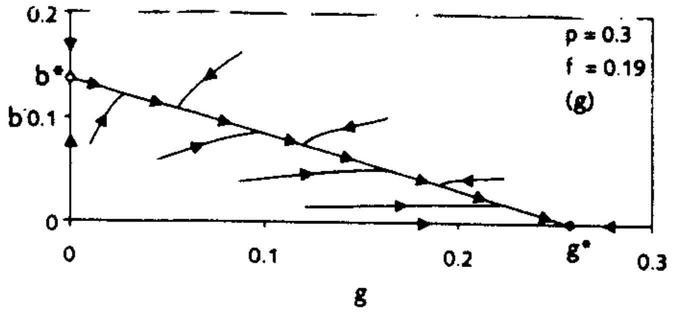
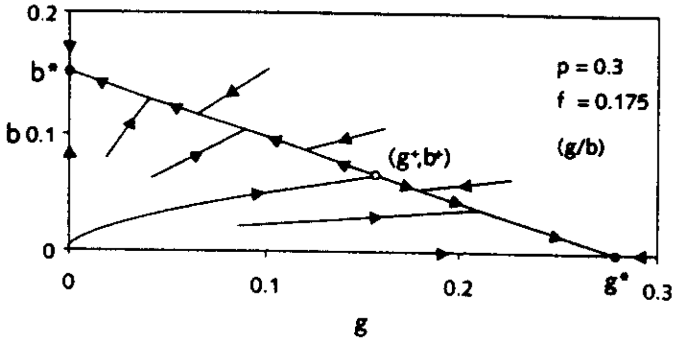

Turbidity
E_{crit}
E_b
Oscillatoriaceae
other algae
P_1
P_2
Total P

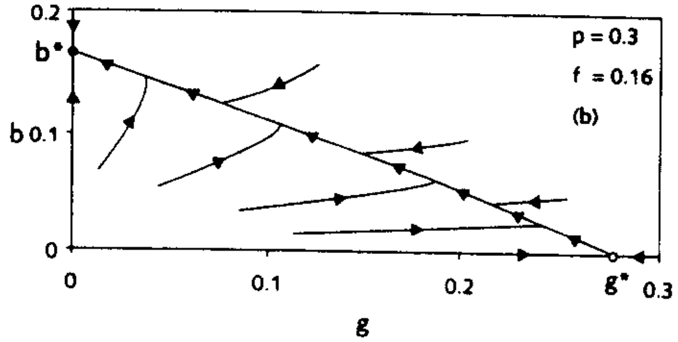
Fig. 7


0.2
b*
b 0.1
0
0
0.1
0.2
g*
0.3
g
p = 0.3
f = 0.19
(g)

(a)


0.2
b*
b 0.1
0
0
0.1
0.2
g*
0.3
g
p = 0.3
f = 0.175
(g/b)
(g⁺,b⁺)

(b)


0.2
b*
b 0.1
0
0
0.1
0.2
g*
0.3
g
p = 0.3
f = 0.16
(b)

(c)

Fig. 8

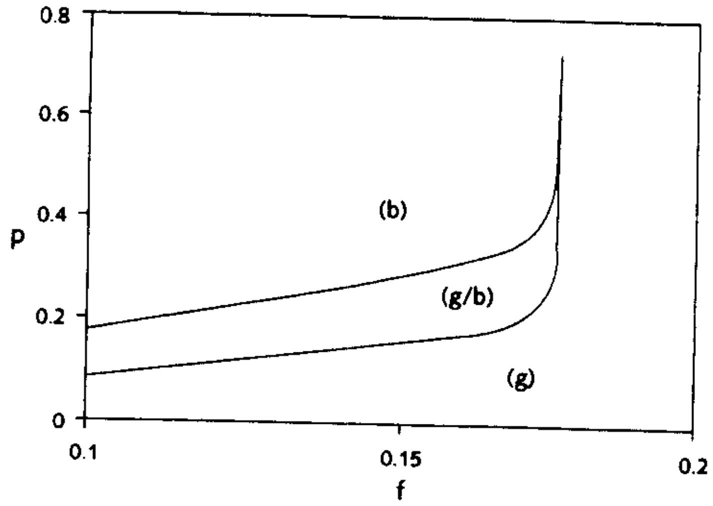
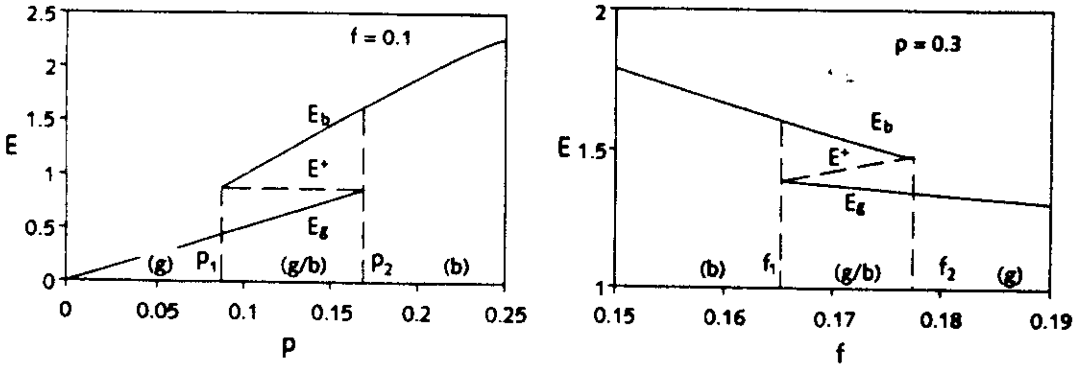


Fig. 9


f = 0.1
E
2.5
2
1.5
1
0.5
0
E_b
E^+
E_g
(g)
p_1
(g/b)
p_2
(b)
0
0.05
0.1
0.15
0.2
0.25
p
p = 0.3
E
2
1.5
1
E_b
E^+
E_g
(b)
f_1
(g/b)
f_2
(g)
0.15
0.16
0.17
0.18
0.19
f

(a)

(b)