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LIGHT-LIMITED GROWTH AND COMPETITION FOR LIGHT IN WELL-MIXED AQUATIC ENVIRONMENTS: AN ELEMENTARY MODEL[1]

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Abstract. Light is never distributed homogeneously since it forms a gradient over biomass. As a consequence, the common theories on nutrient competition are not applicable to competition for light. In this paper, we investigate a model for light-limited growth and competition among phytoplankton species in a mixed water column. The model is based on standard assumptions such as Lambert-Beer's law of light absorption, a Monod equation for carbon uptake, and constant specific carbon losses. By introducing the concept of quantum return, we show that the dynamics of growth and competition can be quantified not only in terms of depth but also directly in terms of light availability. We argue that the crucial measure for phytoplankton growth is not a "critical depth" but a "critical light intensity," I^*_{out}. For each species, I^*_{out} corresponds to the equilibrium light intensity at the bottom of a water column when the species is grown in monoculture. I^*_{out} plays a role similar to the "critical nutrient concentration" R^* used in models of nutrient-limited growth. For a constant light supply, the species with the lowest I^*_{out} will competitively exclude all other species. There are, however, some important differences between R^* and I^*_{out}. Whereas R^* reflects both the local and the total balance between nutrient uptake and nutrient losses, I^*_{out} only reflects the total carbon balance. Moreover, I^*_{out} decreases with increasing light supply, whereas R^* is independent of the nutrient supply. As a consequence, (1) the outcome of competition for light may depend on the light supply, (2) the compensation point is not a good predictor for the outcome of competition, (3) the resource ratio hypothesis does not apply when species compete for both nutrients and light. The outcome of competition for nutrients and light may depend on the nutrient and light supply, on the mixing depth, and on the background turbidity due to inanimate substances.

Key words: carbon balance; compensation point; competitive exclusion; light absorption; nutrient limitation; photosynthesis; phytoplankton; quantum yield; resource competition; spatial heterogeneity.

INTRODUCTION

A variety of competition models leads to the following predictions: If only one resource is limiting, the species that is able to reduce the resource density to the lowest level (R^*) competitively excludes all other species (e.g., Stewart and Levin 1973, Armstrong and McGehee 1980, Butler and Wolkowicz 1985). In case of two limiting resources, coexistence of two species is possible (MacArthur and Levins 1964, Phillips 1973). Stable coexistence requires that each species consumes relatively more of the resource that more limits its own growth (Leon and Tumpson 1975, Butler and Wolkowicz 1987). The outcome of competition for two resources is controlled by the ratio of the rates at which these resources are supplied (Taylor and Williams 1975, Tilman 1982, 1985). Experimental results support these predictions (bacteria: Hansen and Hubbell 1980, Smith 1993; phytoplankton: Tilman 1977, 1981, Holm and Armstrong 1981, Sommer 1989; zooplankton: Rothhaupt 1988).

All these models implicitly or explicitly assume that the limiting resources are distributed homogeneously. As a consequence, they are not applicable to light, since light is never distributed homogeneously but forms a gradient over biomass. In fact, competition for light is mediated by shading and, thus, by the spatial heterogeneity of light created by the competitors themselves. Hence it is unclear whether the principles mentioned above also apply in the context of light limitation. As pointed out by Tilman (1990: 134), "light competition is conceptually more complex than nutrient competition. We do not yet have either rigorous theoretical predictions or experimental results that indicate that a single number, analogous to R^*, can predict the outcome of competition for light. A fuller understanding of light competition remains a major challenge."

In this paper, we consider competition for light among phytoplankton species in a mixed water column. Many models on phytoplankton photosynthesis have been formulated, both for natural systems (e.g., Platt and Sathyendranath 1988, Smith et al. 1989, Fasham et al. 1990, Sakshaug and Slagstad 1991) and algal mass cul-

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TABLE 1. A survey of the symbols used, with their interpretation and dimensions.

Symbol	Interpretation	Dimension
s	depth	m
z	total depth of water column	m
w	biomass density	g/m^3
W	total biomass of water column	g/m^2
I	light intensity	$J \cdot m^{-2} \cdot s^{-1}$
I_c	compensation point	$J \cdot m^{-2} \cdot s^{-1}$
I_{in}	light supply (intensity at top of water column)	$J \cdot m^{-2} \cdot s^{-1}$
I_{out}	light intensity at bottom of water column	$J \cdot m^{-2} \cdot s^{-1}$
$I^*_{out,i}$	critical light intensity at bottom of water column for species i	$J \cdot m^{-2} \cdot s^{-1}$
k	light extinction coefficient	m^2/g
P, L, G	total rate of carbon uptake, loss, gain	$g \cdot m^{-2} \cdot s^{-1}$
p, l, g	specific rate of carbon uptake, loss, gain	1/s
p_{max}	maximum specific carbon uptake rate	1/s
H	half saturation constant of specific carbon uptake rate	$J \cdot m^{-2} \cdot s^{-1}$
q	quantum return	g/J
R	nutrient concentration	g/m^3
R_{in}	nutrient supply concentration	g/m^3
R^*_i	critical nutrient concentration for species i	g/m^3
c	nutrient consumption coefficient	...
h	specific nutrient gain rate	1/s

tures (e.g., Kroon et al. 1989, Evers 1991). Most of these models aim at the quantitative prediction of primary production in specific environments. We are here less concerned with detailed predictions for a particular environment, but aim at obtaining more general, qualitative insights. For this reason, we neglect much of the complexity of real-world systems and keep our model as simple as possible. We make only a few standard assumptions, which can be traced back to the early work of Kok (1952), Sverdrup (1953), and Monsi and Saeki (1953). To our best knowledge, the consequences of these assumptions have never been fully investigated.

The paper is organized as follows. We start by analysing the growth of a monoculture. We first assume that light is only absorbed by biomass. In a next step, we investigate how the growth of a single species is affected by the presence of light absorbers like water and detritus. The results thus obtained provide the basis for understanding competition, where part of the light is absorbed by other species. Consequences for the simultaneous competition for light and nutrients are also investigated. Finally, we discuss the robustness of our results, compare our predictions with published experimental data, and give some hints for further theoretical and experimental research.

LIGHT-LIMITED GROWTH

In this section, we investigate light-limited growth of a monoculture. We assume that light is only absorbed by biomass. In the next section, other light absorbers will also be taken into account. Our notation is provided by Table 1.

Model assumptions

Biomass distribution.—Consider a water column with a vertical light gradient over biomass (Fig. 1). For notational convenience, we focus on a water column with a cross section of one unit area. Vertical positions in this column will be denoted by s, where s is scaled from 0 (top) to z (bottom). We assume that the water column is well mixed such that the biomass density w is independent of depth. Thus the total biomass above depth s is given by the product ws. In particular, the total biomass W of the whole column is given by $W = wz$.

Light absorption.—Light with a certain intensity I_{in} is supplied from above. Let $I(s)$ indicate the light intensity at depth s. $I(s)$ depends on the light supply I_{in} and on the total biomass above s. In fact, according to Lambert-Beer's law:

$$I(s) = I_{in} e^{-kws}, \tag{1}$$

where k represents the light extinction coefficient of biomass. Light that has not been absorbed leaves the water column with a certain intensity $I_{out} = I(z)$. Thus

$$I_{out} = I_{in} e^{-kwz} = I_{in} e^{-kW}.$$

Specific carbon balance.—Light-limited growth depends on the carbon balance, which is determined by carbon uptake and losses. Since light provides the energy for carbon uptake, the "specific" (=per unit biomass) carbon uptake rate, $p(I)$, is a function of the local light intensity I. We assume that $p(I)$ is characterized by a Monod equation:

$$p(I) = p_{max} \frac{I}{H + I}, \tag{2}$$

where p_{max} is the maximum specific carbon uptake rate, and H is the light intensity required for carbon uptake at half the maximum rate.

Carbon losses are due to respiration, excretion, sedimentation, and so on. The specific carbon loss rate, l, is assumed to be constant.

On the local level, growth is governed by the specific carbon gain rate, $g(I)$, the difference between specific carbon uptake and losses:

$$g(I) = p(I) - l. \tag{3}$$

By definition, the compensation point I_c is the light intensity at which specific carbon uptake is exactly balanced by specific carbon losses (Fig. 2):

$$p(I_c) = l \quad \text{or, equivalently,} \quad g(I_c) = 0. \tag{4}$$

In view of Eq. 2, the compensation point is given by

$$I_c = \frac{lH}{p_{max} - l}. \tag{5}$$

Note that I_c is independent of the light supply I_{in} and the light extinction coefficient k.

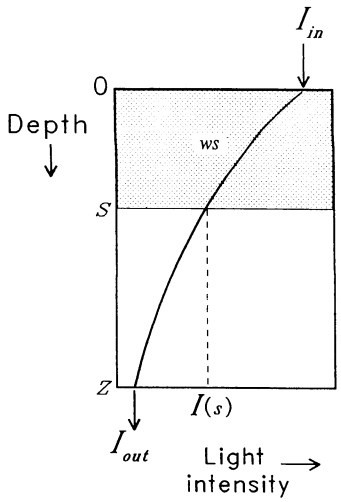

FIG. 1. Illustration of the model structure: light with intensity I_{in} is supplied to a water column. The light intensity at depth s, $I(s)$, results from light absorption by the total biomass, ws, above depth s (z = bottom). Light that has not been absorbed leaves the water column with an intensity I_{out}.

Total carbon balance.—In order to understand biomass growth in the whole water column, we have to consider the total carbon balance. The "local" carbon uptake rate at a given depth s is obtained by multiplying the specific uptake rate at depth s with the biomass density. The "total" carbon uptake rate, P, of the whole water column is then obtained by integrating the local uptake rate over depth:

$$P = \int_0^z p[I(s)]w\, ds. \tag{6}$$

Monsi and Saeki (1953) showed that, given Eqs. 1 and 2, this integral can be solved explicitly (see also Eq. 24):

$$P = \frac{p_{\max}}{k} \ln\left(\frac{H + I_{in}}{H + I_{in}e^{-kW}}\right). \tag{7}$$

Accordingly, P is a function of total biomass, and the derivative of P with respect to W is given by

$$\frac{dP}{dW} = \frac{p_{\max} I_{in} e^{-kW}}{H + I_{in}e^{-kW}} = p(I_{out}). \tag{8}$$

Hence $dP/dW > 0$ and $d^2P/dW^2 < 0$, i.e., P is increasing and concave with respect to total biomass (Fig. 3). P is bounded by the upper asymptote

$$P_\infty = \lim_{W\to\infty} P = \frac{p_{\max}}{k} \ln\left(\frac{H + I_{in}}{H}\right). \tag{9}$$

In other words, a limited energy supply (I_{in}) does not result in an unlimited total carbon uptake.

Similarly, the total carbon loss rate, L, is given by the integral of local carbon loss rate over depth. Since specific carbon losses are assumed to be constant, we get:

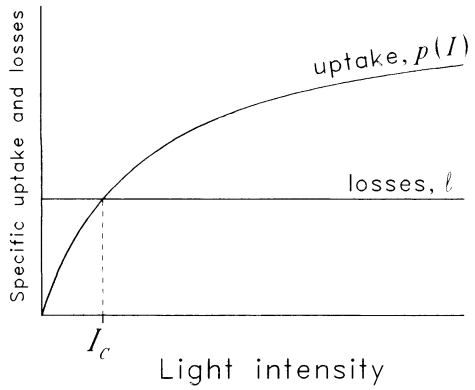

FIG. 2. Specific carbon uptake rate, $p(I)$, and specific carbon loss rate, l, as a function of the light intensity. Specific carbon uptake equals specific carbon losses at the compensation point I_C.

$$L = \int_0^z lw\, ds = lW. \tag{10}$$

Thus L is a linear function of total biomass (Fig. 3), with slope

$$\frac{dL}{dW} = l = p(I_C). \tag{11}$$

The total carbon balance is characterized by the total carbon gain rate, G, which is the difference between the total carbon uptake and loss rates

$$G = \int_0^z g[I(s)]w\, ds = P - L. \tag{12}$$

Growth dynamics.—We assume that the change in total biomass is proportional to the total carbon gain rate: $dW/dt = \alpha G$. For notational convenience, the constant of proportionality α will be incorporated in the parameters $p_{\max}$ and l. Hence, from Eqs. 7 and 10,

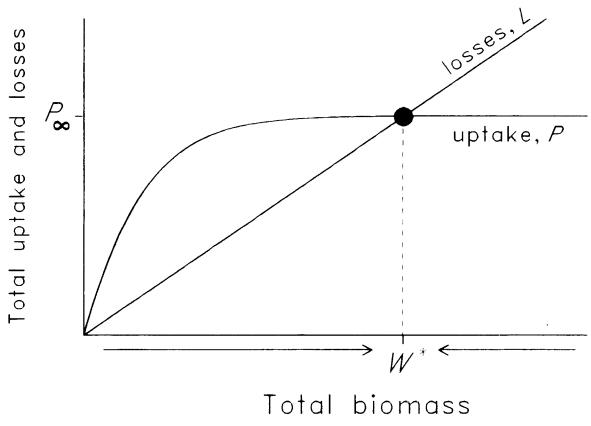

FIG. 3. Total carbon uptake rate, P, and total carbon loss rate, L, as a function of total biomass. Total uptake and losses balance at the globally stable equilibrium W^*.

$$\frac{dW}{dt} = \frac{p_{\max}}{k} \ln\left(\frac{H + I_{in}}{H + I_{in}e^{-kW}}\right) - lW. \quad (13)$$

Due to mixing, the local biomass density w is proportional to total biomass (via $W = wz$). Thus the change in biomass density is also proportional to the total carbon gain rate:

$$\frac{dw}{dt} = \frac{1}{z}\frac{dW}{dt} = \frac{p_{\max}}{kz} \ln\left(\frac{H + I_{in}}{H + I_{in}e^{-kwz}}\right) - lw. \quad (14)$$

Eq. 13 states that the total biomass will increase whenever the total carbon gain is positive (i.e., $P > L$) and it will decrease when G is negative (i.e., $P < L$). The equilibria of Eq. 13 correspond to the intersection points of the functions P and L (Fig. 3). Whenever we discuss the properties of a nontrivial biomass equilibrium, variables such as W, G, and I_{out} will be labeled by a superscript *. Accordingly, a nontrivial biomass equilibrium is characterized by $W^* > 0$ and by

$$P^* = L^* \quad \text{or, equivalently,} \quad G^* = 0. \quad (15)$$

Analysis of the model

Properties of the growth dynamics.—It is obvious that $W = 0$ is a (trivial) equilibrium of Eq. 13, since total carbon uptake and total carbon losses are both zero at $W = 0$. It is also obvious that growth is impossible and the biomass will be driven to zero if the light supply does not exceed the compensation point. Thus, for $I_{in} \leq I_c$, the equilibrium $W = 0$ is globally stable.

Fig. 3 illustrates the situation for a light supply $I_{in} > I_c$. In this case, total carbon uptake exceeds total carbon losses at low biomass. Thus total biomass will increase when low. The functions P and L will always intersect in a unique positive biomass equilibrium W^*, because P is an increasing, concave function bounded by P_z while L increases linearly beyond bounds. W^* is globally stable, since total uptake exceeds total losses below W^* and total losses exceed total uptake above W^*. Comparing the slopes of P and L at the intersection point W^* (see Fig. 3), it is obvious that $(dP/dW) < (dL/dW)$. In view of Eqs. 8 and 11, this is equivalent to $p(I^*_{out}) < p(I_c)$. As a consequence, $I^*_{out} < I_c$. In other words, at the equilibrium W^*, the light intensity at the bottom of a well-mixed water column, I^*_{out}, is reduced beyond the compensation point (cf. Gran and Braarud 1935, Sverdrup 1953). Summarizing, we get:

Result 1. Growth is only possible if the light supply exceeds the compensation point. If I_{in} exceeds I_c, a globally stable, positive biomass equilibrium will be reached at which

$$I_{in} > I_c > I^*_{out} \quad (16)$$

or, equivalently,

$$p(I_{in}) > p(I_c) > p(I^*_{out}). \quad (17)$$

Dependence on the light supply.—W^* is implicitly given by the equilibrium equation

$$\frac{p_{\max}}{k} \ln\left(\frac{H + I_{in}}{H + I_{in}e^{-kW^*}}\right) = lW^*. \quad (18)$$

Intuitively, it is obvious that the equilibrium biomass should become larger with a higher light supply. Analytically, this can be verified by differentiating both sides of Eq. 18 with respect to I_{in}, which yields (see Appendix)

$$\frac{dW^*}{dI_{in}} = \frac{1}{kI_{in}} \frac{p(I_{in}) - p(I^*_{out})}{p(I_c) - p(I^*_{out})}. \quad (19)$$

In view of Eq. 17, dW^*/dI_{in} is indeed positive.

How I^*_{out} will change with the light supply is less obvious. For a fixed biomass, I_{out} increases with I_{in}. The equilibrium biomass, however, is not fixed but is also increasing with I_{in}. Differentiation of $I^*_{out} = I_{in}e^{-kW^*}$ yields

$$\frac{dI^*_{out}}{dI_{in}} = e^{-kW^*}\left(1 - kI_{in}\frac{dW^*}{dI_{in}}\right).$$

Together with Eqs. 19 and 17 this implies

$$\frac{dI^*_{out}}{dI_{in}} = \frac{I^*_{out}}{I_{in}}\left[\frac{p(I_{in}) - p(I_c)}{p(I^*_{out}) - p(I_c)}\right] < 0. \quad (20)$$

Thus I^*_{out} decreases with increasing I_{in}. In other words, light absorption by the increased biomass overcompensates for the effect of an increased light supply.

Result 2. The equilibrium biomass W^* is positively related to the light supply I_{in}. I^*_{out} is negatively related to I_{in}.

Dependence on the extinction coefficient.—We can also ask how, given a certain light supply, I^*_{out} and W^* will change with a change in the light extinction coefficient k. For a fixed biomass, it is obvious that a higher k leads to a lower I_{out}. The equilibrium biomass, however, will change with a change in k. Rearranging Eq. 18 leads to

$$\frac{1}{kW^*} \ln\left(\frac{H + I_{in}}{H + I_{in}e^{-kW^*}}\right) = \frac{l}{p_{\max}}. \quad (21)$$

For a fixed light supply I_{in}, the left-hand side of Eq. 21 is a decreasing function of kW^*, whereas the right-hand side is constant. Hence Eq. 21 has a unique solution in terms of kW^*. The uniqueness of kW^* implies that W^* is inversely proportional to the light extinction coefficient k. In other words, the product kW^* is independent of the value of k. Since, for a fixed I_{in}, I^*_{out} only depends on kW^*, we arrive at the counterintuitive result that I^*_{out} is independent of the light extinction coefficient.

Result 3. The equilibrium biomass W^* is inversely proportional to the light extinction coefficient k. I^*_{out} is independent of k.

Notice that we have treated k as a parameter that can be varied independently of H, $p_{\max}$, and l. In reality,

however, H and p_{max} are related to k since light absorption provides the energy for carbon uptake. The basic message of result 3 is that k does not directly affect I^*_{out}, but at most indirectly via the parameters determining the shape of the $g(I)$ curve.

An alternative look at the light gradient

Until now, the total carbon uptake rate has been viewed as an integral over depth, which is the usual approach in models of phytoplankton photosynthesis. We argue that a better intuitive understanding of light-limited growth is obtained if photosynthesis is not interpreted in terms of depth but in terms of light availability. An obvious reason is that photosynthesis is a direct function of light availability while it is only indirectly related to depth. Moreover, the light availability at a certain depth is not constant. In particular, it will change due to the increased turbidity caused by a growing phytoplankton population.

The total carbon uptake rate P can easily be written as an integral over light intensity. According to Lambert-Beer's law,

$$\frac{dI}{ds} = -kwI(s). \tag{22}$$

Thus Eq. 6 can be rewritten as

$$P = \int_0^z \frac{p[I(s)]w}{-kwI(s)} \frac{dI}{ds}\, ds = \int_{I_{out}}^{I_{in}} \frac{p(I)}{kI}\, dI, \tag{23}$$

where the exchange of the borders of integration results from the minus sign in Eq. 22. This representation allows a simple proof of Eq. 7:

$$P = \frac{p_{max}}{k} \int_{I_{out}}^{I_{in}} \frac{1}{H + I}\, dI = \frac{p_{max}}{k} \ln\left(\frac{H + I_{in}}{H + I_{out}}\right). \tag{24}$$

The integrand in Eq. 23, $p(I)/kI$, has a clearcut interpretation. It corresponds to the quantum yield (cf. Kirk 1983), since it expresses the carbon uptake per unit of light (i.e., per quantum) absorbed. Notice that the quantum yield is not constant but negatively related to the light intensity. This can be explained by the limited processing capacity of a photosynthetic unit. At high light intensities, many absorbed quanta cannot be utilized for photosynthesis since the photosynthetic units are still processing the energy obtained from previously absorbed photons (e.g., Dubinsky et al. 1986, Sakshaug et al. 1989).

Quantum yield only considers the efficiency of carbon uptake. For a proper understanding of light-limited growth, however, carbon losses must be taken into account. For this reason, we propose the concept of "*net* quantum yield" or "quantum return" $q(I)$, which corresponds to the carbon gain per unit of light absorbed:

$$q(I) = \frac{g(I)}{kI}. \tag{25}$$

The total carbon gain G can now be written as the integral of quantum return over the light gradient:

$$G = \int_{I_{out}}^{I_{in}} \frac{g(I)}{kI}\, dI = \int_{I_{out}}^{I_{in}} q(I)\, dI. \tag{26}$$

In view of Eq. 4, the quantum return is positive if the light intensity exceeds the compensation point and negative if the light intensity is below the compensation point. This provides the key to a better insight into the equilibrium properties of light-limited growth. The equilibrium equation $G^* = 0$ can be written in the form

$$G^* = \int_{I_C}^{I_{in}} q(I)\, dI + \int_{I^*_{out}}^{I_C} q(I)\, dI = 0. \tag{27}$$

The first integral in Eq. 27 is positive, since it focuses on the light intensities above the compensation point. The second integral is negative, because it only includes light intensities below the compensation point. Result 1 in the preceding paragraph ($I^*_{out} < I_C < I_{in}$) simply reflects the balance between positive quantum returns above I_C and negative quantum returns below I_C.

An increase of the light supply I_{in} leads to an increase to the total quantum return above the compensation point (since I_C is independent of I_{in}). At equilibrium, the increased positive quantum return above I_C must be balanced by an increased negative quantum return below I_C. Accordingly, the second integral in Eq. 27 must become more negative, i.e., I^*_{out} must decrease. Hence the decrease of I^*_{out} with increasing I_{in} (result 2) reflects the fact that, in equilibrium, the increased biomass above I_C has to be balanced by an increased biomass below I_C.

Competition for Light

Light-limited growth in mixtures

Light absorption.—In the previous section, we considered the light-limited growth of a monoculture where light was only absorbed by biomass. We now introduce other light absorbers like water, detritus, and competing species. For notational convenience, we use the same symbols for biotic and abiotic light absorbers. The light absorbers will be indicated by subscripts such as i and j. Thus, k_j and w_j denote the light extinction coefficient and the density of light absorber j, respectively. Again, we assume that light absorption obeys Lambert-Beer's law:

$$I(s) = I_{in} e^{-\sum k_j w_j s}. \tag{28}$$

Growth dynamics.—We assume that the growth of all organisms only depends on light availability. In particular, there is no direct interference between different species, there are no toxic interactions, and growth is not limited by other resources. Hence the biomass growth of light absorber i corresponds to its total carbon gain rate, G_i, which is only related to other light absorbers via $I(s)$:

$$\frac{dW_i}{dt} = G_i = \int_0^z g_i[I(s)]w_i\, ds. \qquad (29)$$

For inanimate light absorbers, we assume that $g_i = 0$, i.e., they neither grow nor decay.

Partitioning of the light gradient.—According to Eq. 28, light absorption is governed by the equation

$$\frac{dI}{ds} = -\left(\sum k_j w_j\right) I(s). \qquad (30)$$

This implies that the total carbon gain of a species can be rewritten as an integral over light intensity:

$$G_i = \int_0^z \frac{g_i[I(s)]w_i}{-(\Sigma\, k_j w_j)I(s)} \frac{dI}{ds}\, ds = \frac{k_i w_i}{\Sigma\, k_j w_j} \int_{I_{\text{out}}}^{I_{\text{in}}} \frac{g_i(I)}{k_i I}\, dI.$$

In view of $W_i = w_i z$ and the definition of quantum return, we get

$$G_i = \frac{k_i W_i}{\Sigma\, k_j W_j} \int_{I_{\text{out}}}^{I_{\text{in}}} q_i(I)\, dI. \qquad (31)$$

This equation has a clearcut interpretation. The first term, $k_i W_i / \Sigma\, k_j W_j$, describes the relative contribution of species i to the total light absorption. The second term, $\int_{I_{\text{out}}}^{I_{\text{in}}} q_i(I)\, dI$, corresponds to the total carbon gain that species i would have attained in the same light gradient when grown in monoculture (i.e., in the absence of other light absorbers). Thus Eq. 31 just states which part of the total light absorption is available for the carbon gain of species i.

In order to stress the dependence of G_i on the light gradient, and to emphasize the relation between total gain in mixture and total gain in monoculture, we write Eq. 31 as

$$G_i(I_{\text{out}}) = \frac{k_i W_i}{\Sigma\, k_j W_j} G_{i,\text{mono}}(I_{\text{out}}). \qquad (32)$$

(A similar partitioning was derived by Bannister 1974.)

Light requirements for growth.—Let $W^*_{i,\text{mono}}$ denote the equilibrium biomass of species i in monoculture (i.e., without any other light absorbers), and $I^*_{\text{out},i}$ the resulting light intensity at the bottom of the water column:

$$I^*_{\text{out},i} = I_{\text{in}} e^{-k_i W^*_{i,\text{mono}}}. \qquad (33)$$

In the previous section, we have shown that $G_{i,\text{mono}}$ is positive if $I_{\text{out}} > I^*_{\text{out},i}$, and negative if $I_{\text{out}} < I^*_{\text{out},i}$. The same holds true for the total carbon gain rate G_i in a multispecies mixture, since G_i has the same sign as $G_{i,\text{mono}}$ (see Eq. 32). Hence, in view of the relation between G_i and the growth dynamics, we obtain the following key result:

Result 4. The equilibrium value of I_{out} for species i in monoculture, $I^*_{\text{out},i}$, specifies when this species will grow in mixture: Species i will increase if $I_{\text{out}} > I^*_{\text{out},i}$, it will decrease if $I_{\text{out}} < I^*_{\text{out},i}$, and it will remain stationary if $I_{\text{out}} = I^*_{\text{out},i}$.

Notice that the condition for stationarity, $I_{\text{out}} = I^*_{\text{out},i}$, can be written in the form

$$I_{\text{out}} = I_{\text{in}} e^{-\Sigma k_j W_j} = I_{\text{in}} e^{-k_i W^*_{i,\text{mono}}} = I^*_{\text{out},i}.$$

As a consequence, for $W_i > 0$, we get

$$\frac{dW_i}{dt} = 0 \quad \text{if} \quad \sum k_j W_j = k_i W^*_{i,\text{mono}}. \qquad (34)$$

Growth in the presence of inanimate light absorbers

When talking about a monoculture, we have implicitly neglected light absorption by water, detritus, and other dead substances. Let us now consider the effects of such inanimate light absorbers on the growth of a single species i. In the absence of species i, the inanimate light absorbers would reduce light at the bottom of the water column to the "background level"

$$I_{\text{out,bg}} = I_{\text{in}} e^{-\sum_{j \neq i} k_j W_j}.$$

In view of result 4 and Eq. 34, $I_{\text{out,bg}}$ provides the threshold level for the growth of species i:

Result 5. The equilibrium value of I_{out} for species i in monoculture, $I^*_{\text{out},i}$, specifies whether this species is able to grow in mixture with inanimate light absorbers. Growth is only possible if

$$I^*_{\text{out},i} < I_{\text{out,bg}}. \qquad (35)$$

If Eq. 35 holds true, species i will reach a globally stable, positive biomass equilibrium W^*_i. At this equilibrium, I_{out} attains the same level $I^*_{\text{out},i}$ as would have been attained in monoculture. The equilibrium biomass W^*_i in the presence of inanimate light absorbers is related to the equilibrium biomass $W^*_{i,\text{mono}}$ via

$$W^*_i = W^*_{i,\text{mono}} - \frac{1}{k_i} \sum_{j \neq i} k_j W_j.$$

Thus the light requirements of a phytoplankton species i can be characterized by a "critical light intensity" $I^*_{\text{out},i}$. In our simple model at least, this critical light intensity is independent of the turbidity caused by other light absorbers.

Competition

Competitive exclusion.—Consider n species competing for light at a constant light supply. In monoculture, each species i would induce an equilibrium light intensity $I^*_{\text{out},i}$. Result 4 shows that, in a mixture, equilibrium coexistence is only possible if several species have identical values $I^*_{\text{out},i}$. Since this is rather unlikely and structurally unstable, the possibility of equilibrium coexistence can be neglected.

Let the species be labeled such that $I^*_{\text{out},1} < I^*_{\text{out},2} < \ldots < I^*_{\text{out},n}$. As long as $I_{\text{out}} > I^*_{\text{out},1}$, species 1 will increase. Hence, in the long run, species 1 will be able to reduce I_{out} below $I^*_{\text{out},2}$. When $I^*_{\text{out},1} < I_{\text{out}} < I^*_{\text{out},2}$,

all species, except species 1, will decrease. This process will continue until all species, except species 1, are driven to extinction while species 1 approaches its biomass equilibrium at which $I_{out} = I^*_{out,1}$. (A more general, formal proof of global stability is given in Weissing and Huisman [1994].) Summarizing,

Result 6. Under a constant light supply, the species i with lowest $I^*_{out,i}$ will competitively exclude all other species. In other words, light absorption is maximized by competition for light.

As an illustration, consider competition for light between two species. In view of Eq. 34, the zero isocline of species i (where $i = 1, 2$) is given by

$$k_1 W_1 + k_2 W_2 = k_i W^*_{i,mono}. \qquad (36)$$

The competition dynamics is indicated by the phase portrait of Fig. 4. The qualitative behavior resembles that of the competition model originally derived by Volterra (1928). Eq. 36 implies that, as in Volterra's classical model, the zero isoclines of both species have identical slopes (Fig. 4). Hence they cannot intersect, which again illustrates that equilibrium coexistence is impossible. Instead, the species with the outermost zero isocline (i.e., the species with the higher value $k_i W^*_{i,mono}$) will competitively exclude the other species, because it is able to reduce I_{out} to the lowest level.

Dependence on the light supply.—We have seen that $I^*_{out,i}$, as measured in monoculture, predicts the outcome of competition for light. We have also seen that $I^*_{out,i}$ is negatively related to I_{in} (result 2). Hence it is conceivable that the outcome of competition for light depends on the light supply. That this may indeed occur, is illustrated in Fig. 5. In Fig. 5A, the specific carbon gain rates of two species, 1 and 2, are depicted as functions of the light intensity. If one of the two species had a uniformly higher specific carbon gain

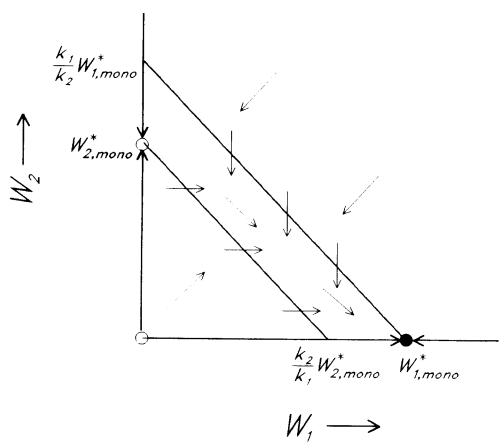

FIG. 4. Zero isoclines of two species competing for light in a mixed water column. Species 1 competitively excludes species 2, because $k_1 W^*_{1,mono} > k_2 W^*_{2,mono}$ (which implies $I^*_{out,1} < I^*_{out,2}$).

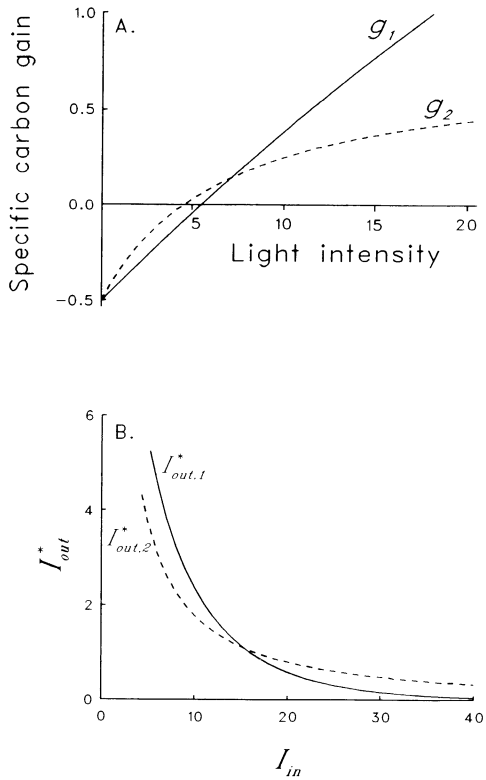

FIG. 5. (A) Specific carbon gain, g_i, as a function of the light intensity, for species 1 and 2. (B) Relation between the light supply I_{in} and the critical light intensity I^*_{out} of these two species. For a given light supply, the species with lowest I^*_{out} competitively excludes the other species. Thus species 1 will win the competition if $I_{in} > 16$, and species 2 will win if $I_{in} < 16$. (Parameter values: $p_{max,1} = 10$; $p_{max,2} = 1.25$; $H_1 = 100$; $H_2 = 6.5$; $l_1 = l_2 = 0.5$. Light extinction coefficients are not given since I^*_{out} is independent of k.)

than the other species, the former would always competitively exclude the latter. Here, however, species 2 has a higher specific carbon gain at low light intensities, whereas species 1 has a higher specific carbon gain at high light intensities. Correspondingly, $I^*_{out,2}$ is smaller than $I^*_{out,1}$ at a low light supply, and $I^*_{out,1}$ is smaller than $I^*_{out,2}$ at a high light supply (Fig. 5B). Thus species 2 will win the competition at a low light supply, whereas species 1 will win at a high light supply.

Result 7. The winner of competition for light may depend on I_{in}.

Result 7 may have important implications for competition for light under a seasonally fluctuating light supply. In fact, the seasonal change of I_{in} may induce seasonal changes in the competitive dominance of a species (e.g., Hutchinson 1967, Stockner 1968).

Competition and the compensation point.—According to result 7, the outcome of competition may depend on the light supply. In contrast, the compensation point of a species is independent of the light supply (see Eq. 5). Hence it is conceivable that the species with lowest compensation point is competitively excluded. In fact,

in the example considered in Fig. 5, species 2 has the lowest compensation point, but will be competitively excluded at a high light supply.

Result 8. The compensation point is not a good predictor for the outcome of competition for light. The species with lowest compensation point may be competitively excluded by a species with lower $I^*_{\text{out},i}$.

This result is not as counterintuitive as it may appear. A compensation point only indicates the local carbon balance at a single light intensity. It does not include information on other parts of the light gradient. In contrast, $I^*_{\text{out},i}$ "summarizes" the total carbon balance, and thereby the dynamics over the whole light gradient.

Competition for Nutrients and Light

Light limitation vs. nutrient limitation

At this point, it may be useful to compare our model of light limitation with models of nutrient limitation. Competition for nutrients in a mixed water column is usually modeled in terms of the nutrient concentration R and biomass densities w_i. Following Armstrong and McGehee (1980), competition for a homogeneously distributed nutrient may be characterized by the following dynamics:

$$\frac{dw_i}{dt} = h_i(R)w_i, \tag{37}$$

$$R = R_{\text{in}} - \sum c_i w_i. \tag{38}$$

Here the "specific nutrient gain rate" of species i is an increasing function h_i of the nutrient concentration R, R_{in} denotes the nutrient supply concentration, and the c_i relate nutrient consumption to biomass production. Eq. 38 can be derived from a steady-state approximation of the usual chemostat models (cf. Appendix A of Armstrong and McGehee 1980).

To elucidate the correspondence with our model of light competition, we write Lambert-Beer's law in logarithmic form and the growth dynamics (Eq. 29) in terms of biomass densities (see Eq. 14):

$$\frac{dw_i}{dt} = \frac{1}{z}\int_0^z g_i[I(s)]w_i\, ds, \tag{39}$$

$$\ln(I_{\text{out}}) = \ln(I_{\text{in}}) - \sum k_i w_i z. \tag{40}$$

Notice that the crucial difference between the two models is related to the spatial heterogeneity of the light gradient: the two models would be essentially equivalent if $I(s)$ would not depend on s.

The growth dynamics (Eq. 37) of species i can be characterized by the relation between nutrient concentration R and the "critical nutrient concentration" R_i^*, which is defined by $h_i(R_i^*) = 0$. R_i^* resembles $I^*_{\text{out},i}$ in that species i will increase if $R > R_i^*$, it will decrease if $R < R_i^*$, and it will remain stationary if $R = R_i^*$ (compare with result 4). Accordingly, R_i^* can predict the outcome of competition: if species compete for a single nutrient in a mixed water column, the species with lowest R_i^* competitively excludes all other species (Armstrong and McGehee 1980, Tilman 1982).

The definition of R_i^* is analogous to that of the compensation point $I_{C,i}$, which is defined by $g_i(I_{C,i}) = 0$. We have shown that the compensation point is not a good predictor for the outcome of competition for light because it only indicates the local carbon balance, not the total carbon balance (result 8). In contrast, R_i^* does predict the outcome of competition. The reason is that, in the case of a homogeneously distributed resource, the local balance corresponds to the total balance. Analogous to $I_{C,i}$, R_i^* is independent of the nutrient supply R_{in}. Hence, the outcome of competition for a single nutrient will be independent of the nutrient supply. In contrast, $I^*_{\text{out},i}$ is a function of I_{in} and the outcome of competition for light may depend on the light supply.

A graphical approach to competition for nutrients and light

Typically, species compete for several resources at the same time. The outcome of competiton for two homogeneously distributed resources can be predicted on the basis of zero isoclines, consumption vectors, and a resource supply point (Leon and Tumpson 1975, Taylor and Williams 1975; for a survey see Tilman 1982). We will now discuss whether this graphical approach can be applied to competition for light and a single nutrient in a mixed water column.

Zero isoclines.—Suppose that light and the limiting nutrient are "perfectly essential" resources (sensu Tilman 1982):

$$\frac{dw_i}{dt} = \min\left\{h_i(R)w_i;\ \ \frac{1}{z}\int_0^z g_i[I(s)]w_i\, ds\right\}. \tag{41}$$

The minimum function implies that the growth rate of species i is either nutrient limited or light limited. In Fig. 6, the zero isocline of species i, specified by $dw_i/dt = 0$, is depicted in the (R, I_{out}) plane. In view of Eq. 41, the zero isocline has a right angle corner at the point (R_i^*, $I^*_{\text{out},i}$). Remember that R_i^* is independent of the nutrient supply R_{in}, while $I^*_{\text{out},i}$ depends on the light supply I_{in}. As a consequence, for each different I_{in} a new zero isocline has to be derived.

Consumption vectors.—The graphical approach makes use of a linear relation between biomass and consumption. In this case, the course of resource reduction can be predicted on the basis of a consumption vector. In contrast to nutrient consumption (see Eq. 38), light "consumption" will only be linearly related to biomass if the light intensity is measured on a logarithmic scale (see Eq. 40). One unit of biomass density w_i will reduce R by an amount c_i and $\ln(I_{\text{out}})$ by an amount $k_i z$. The slope of the consumption vector in Fig. 6 is therefore given by the ratio between light extinction $k_i z$ and nutrient consumption c_i.

Supply point.—The supply point is the third ingredient required for predicting the outcome of competition. It is given by the values of R and I_{out} in the absence of competing species. Thus the supply point provides the "starting point" for the resource consumption vectors. In Fig. 6, the supply point is positioned at (R_{in}, I_{in}), thereby implicitly assuming that light absorption by inanimate substances can be neglected. If inanimate light absorbers were also present, the light supply available for biomass growth would be reduced from I_{in} to $I_{out,bg}$ (cf. result 5). Hence, in the presence of inanimate light absorbers the supply point should be positioned at $(R_{in}, I_{out,bg})$.

Predictions.—With the modifications discussed above, we arrive at similar predictions as the "standard" graphical approach. Given the isocline pattern of the competing species, the slopes of their consumption vectors and the position of the supply point, three different situations are possible: (1) all species are nutrient limited and the species with lowest R_i^* outcompetes the others, (2) all species are light limited and the species with lowest $I_{out,i}^*$ displaces all others, and (3) some species are nutrient limited and others light limited. In the latter case, at most two species may coexist. Coexistence is stable if, at equilibrium, each of the two species consumes relatively more of the resource that more limits its own growth (cf. Leon and Tumpson 1975, Tilman 1982, Butler and Wolkowicz 1987).

Departures from the "standard" approach.—There are some important differences between competition for two nutrients and competition for one nutrient and light. The consumption vectors depend not only on species characteristics, but also on the depth z of the mixed water column (see Fig. 6). The basic reason is that nutrient consumption is related to resource concentrations (amount per unit volume), whereas light absorption is related to a resource flux (irradiation per unit area). Furthermore, the position of the supply point depends not only on the nutrient and light supply, but also on the turbidity caused by inanimate substances. Thus, the outcome of competition is not only determined by the nutrient and light supply, but also by the mixing depth and the background turbidity.

In the standard approach, the three possible equilibrium regimes (prevalence of species 1, prevalence of species 2, or coexistence, respectively) are separated by straight lines (Fig. 7A). The slopes of these lines are given by the consumption vectors. As a consequence, the outcome of competition is controlled by the ratio of the resource supplies (Tilman 1982, 1985). In the context of competition for nutrients and light, however, this "resource ratio hypothesis" no longer holds true (Fig. 7B–D). The basic reason is that, via the dependence of $I_{out,i}^*$ on I_{in}, the isocline pattern depends on the position of the supply point. We see no simple graphical procedure that reveals the relation between I_{in} and the coexistence region.

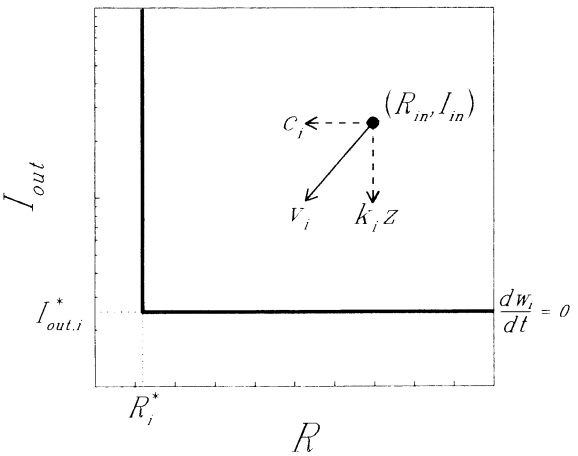

FIG. 6. Graphical representation of the growth of species i when limited by light and a single nutrient. The graph consists of a zero isocline characterized by R_i^* and $I_{out,i}^*$, a supply point (R_{in}, I_{in}), and a consumption vector v_i. Since $I_{out,i}^*$ is a function of I_{in}, the position of the isocline depends on the position of the supply point. In view of Lambert-Beer's law, I_{out} is measured on a logarithmic scale.

Fig. 7B–D are based on computer simulations and illustrate the equilibrium regimes for three different parameter constellations. In each case, the outcome of competition is shown for various combinations of the nutrient and light supply. In all three cases, species 1 has the lowest R^* and is, thus, the superior nutrient competitor. In Fig. 7B, species 2 has the lowest I_{out}^* for all light supplies and is therefore the superior light competitor. Coexistence occurs if species 1 is light limited and species 2 nutrient limited. Notice that the coexistence regions in Fig. 7A and B look rather similar, but even if I_{in} is scaled logarithmically, the coexistence region of Fig. 7B is not bounded by straight lines. In Fig. 7C and D, the picture is further complicated, since it depends on the light supply I_{in} which species is the superior competitor for light. Fig. 7C shows a situation where species 1 has the lowest I_{out}^* for a low I_{in}, while species 2 has the lowest I_{out}^* for a high I_{in}. As a consequence, there is a threshold value of I_{in} below which coexistence is impossible because species 1 is the superior competitor for both resources. Finally, in Fig. 7D, species 2 is the superior light competitor for a low I_{in}, but an inferior light competitor at high I_{in}. Now coexistence is impossible above a certain threshold value for I_{in}. Summarizing,

Result 9. If species compete for light and a single nutrient in a mixed water column, stable coexistence of two species is possible if one species is nutrient limited and the other species is light limited. For a fixed light supply, the outcome of competition can be predicted from a graphical isocline approach, where I_{out} is scaled logarithmically. But the isocline pattern depends on the light supply and the resource ratio hypothesis does not hold. Furthermore, the outcome of competition does not only depend on the nutrient and

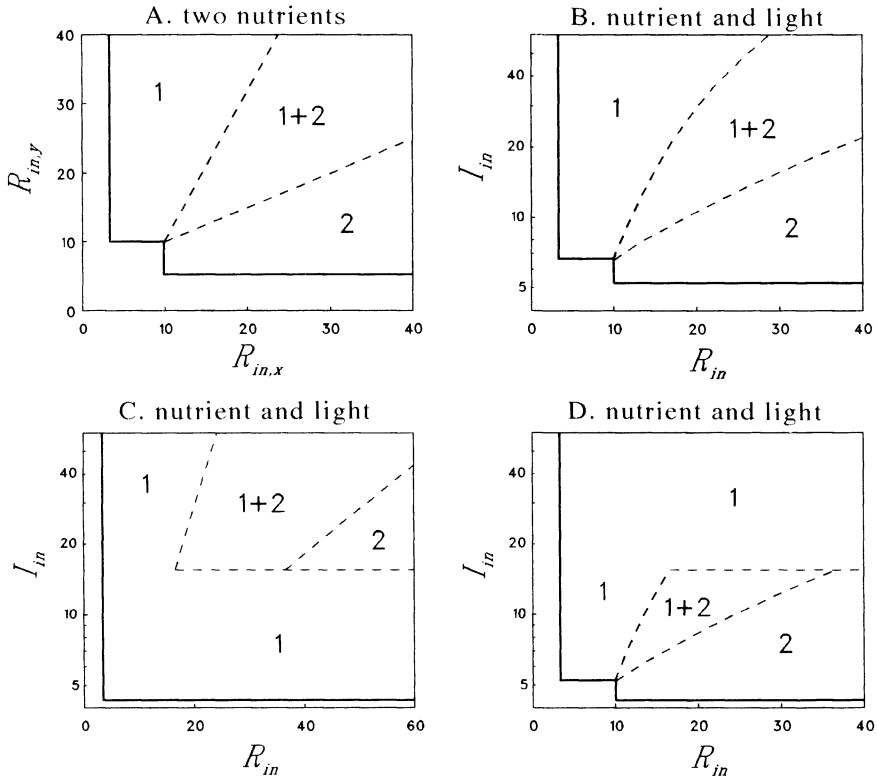

FIG. 7. Competition between two species for two resources in a mixed water column. The graphs represent the outcome of competition as a function of the resource supplies. The labels "1" and "2" indicate the regions in parameter space where either species 1 or species 2 will win the competition. Coexistence will occur in region "1 + 2." (A) A typical example of competition for two nutrients, X and Y, for various combinations of the nutrient supplies $R_{in,X}$ and $R_{in,Y}$. (B–D) Three examples of competition for light and a single nutrient. Note that the light supply I_{in} is measured on a logarithmic scale, whereas the nutrient supply R_{in} is measured on a linear scale. Isoclines cannot be drawn, since they depend on I_{in}. (B–D) are based on a specific version of Eq. 41:

$$\frac{dw_i}{dt} = \min\left[\frac{r_i R}{M_i + R} w_i;\quad \frac{k_i w_i}{k_1 w_1 + k_2 w_2}\frac{p_{\max,i}}{k_i z}\ln\left(\frac{H_i + I_{in}}{H_i + I_{out}}\right)\right] - l_i w_i,$$

where $$R = R_{in} - c_1 w_1 - c_2 w_2 \quad \text{and} \quad I_{out} = I_{in} e^{-(k_1 w_1 + k_2 w_2)z}.$$

Parameter values: (B) $p_{max,1} = 8$; $p_{max,2} = 10$; $H_1 = H_2 = 100$, (C) $p_{max,1} = 1.25$; $p_{max,2} = 10$; $H_1 = 6.5$; $H_2 = 100$, (D) $p_{max,1} = 10$; $p_{max,2} = 1.25$; $H_1 = 100$; $H_2 = 6.5$, (B–D) $r_1 = 2$; $r_2 = 1$; $M_1 = M_2 = 10$; $l_1 = l_2 = 0.5$; $z = 1$; $c_1 = 0.02$; $c_2 = 0.04$; $k_1 = 0.008$; $k_2 = 0.004$.

light supply, but also on the background turbidity and the mixing depth.

DISCUSSION

Implications of a light gradient

Competitive interactions are often indirect: organisms consume resources and thereby deplete the resource availability for their competitors. Consequently, a proper understanding of resource competition requires an explicit consideration of the resource dynamics (Stewart and Levin 1973, Tilman 1982). In the context of competition for light, competitive interactions are mainly mediated by mutual shading. Hence the light gradient is not static but dynamic, since it is at least partly generated by the phytoplankton species themselves. In our opinion, a dynamic description of the light gradient is a prerequisite for the understanding of competition for light.

The usual approach towards algal photosynthesis focuses on the prediction of aquatic primary production but does not promote a firm intuitive insight into the dynamics of competition for light. In most studies, local photosynthesis is directly related to depth. This is reflected in concepts like "compensation depth" and "critical depth" (e.g., Sverdrup 1953, Smetacek and Passow 1990, Platt et al. 1991). The critical depth, for example, is defined as the maximal depth of a mixed surface layer that still allows phytoplankton growth. A problem with this approach is that the critical depth depends on turbidity and therefore on phytoplankton biomass. A growing phytoplankton population reduces the critical depth by shading itself.

We have shown that photosynthesis can be quantified not only in terms of depth, but also directly in terms of light availability. This revealed that, in our model at least, the dynamic properties of light-limited

growth can be characterized by a "critical light intensity" I^*_{out}. For each species, I^*_{out} corresponds to the equilibrium light intensity at the bottom of a mixed water column when the species is grown in monoculture. In contrast to the critical depth, the critical light intensity is independent of turbidity. Accordingly, a critical light intensity should provide a better reference point for the light requirements of a phytoplankton species than a critical depth.

A key result of the present paper relates I^*_{out} as measured in monoculture to the light requirements of a species when grown in mixture with other light absorbers. Since growth in a mixture will proceed until the resource availability has been depleted to the minimal resource requirements, I^*_{out} can predict the outcome of competition for light. In contrast to the compensation point I_c, which only indicates a local balance between carbon uptake and carbon losses, I^*_{out} is able to summarize the growth dynamics over the whole light gradient. The critical light intensity I^*_{out} plays a similar role for light competition as the "critical nutrient concentration" R^* does for nutrient competition. There is, however, an important difference between R^* and I^*_{out}. Whereas R^* is independent of the nutrient supply, I^*_{out} is negatively related to the light supply. As a consequence, the outcome of competition for light may depend on the light supply. Furthermore, knowledge of the ratio between nutrient supply and light supply is not sufficient to predict the outcome of competition for nutrients and light. Hence, Tilman's (1982, 1985) "resource ratio hypothesis" does not hold in the context of light competition.

Tests of the model predictions

From rather standard assumptions, we have derived a number of clearcut, testable predictions: (1) the outcome of competition for light can be inferred from growth characteristics measured in monoculture, i.e., the species with lowest I^*_{out} competitively excludes all other species; (2) I^*_{out} does not depend on the amount of other light absorbers; (3) I^*_{out} is negatively related to the light supply; (4) the outcome of competition for light depends on the light supply; (5) for a fixed light supply, the outcome of competition for nutrients and light can be inferred from a graphical isocline approach; (6) the outcome of competition for nutrients and light depends on the nutrient and light supply, on turbidity, and on the size and shape of the culture vessel; and (7) stable coexistence of two species is possible if one species is nutrient limited and the other species is light limited. Of course, a simple model cannot cover the full complexity of any natural or experimental system. It is nevertheless worthwhile to investigate to what extent the behavior of our model is matched by the behavior of light-limited phytoplankton populations. Unfortunately, we are not aware of any empirical study where the crucial information on I^*_{out} is presented in such a way that our predictions could be fully evaluated.

In a study of the phytoplankton spring blooms in various regions of the North Sea, the light requirements for algal growth have been characterized in terms of a critical light intensity (Gieskes and Kraay 1975). Gieskes and Kraay observed considerable variation in the onset of the spring blooms, which was related to the background turbidity of the water. Independent of turbidity, however, the spring blooms always started at a similar depth-averaged light intensity of ≈ 21 W/m^2 (see also Riley 1957).

In the context of algal mass cultures, Evers (1991) constructed a model that is based on similar assumptions as our model. He showed that data from Van Liere and Mur (1979) on steady-state biomass and specific light energy uptake of *Oscillatoria agardhii* fit well to his model. This gives hope that our model, too, captures some essential features of light-limited growth. Evers considered, however, a two-dimensional light gradient since the experiments of Van Liere and Mur were performed with continuous cultures evenly illuminated from all sides. Under these conditions our predictions on I^*_{out} cannot be evaluated, because I^*_{out} is only defined for a one-dimensional light gradient.

Only a few competition experiments with light-limited continuous cultures have been performed. In all experiments we are aware of, competitive exclusion has been found. Zevenboom et al. (1981) found that a nonheterocystous mutant of the nitrogen-fixing cyanobacterium *Aphanizomenon flos-aquae* had a much higher specific growth rate than the wild type at all light intensities. As expected, under light-limited conditions the wild type was competitively displaced by the mutant. Mur et al. (1977) studied competition for light between the green alga *Scenedesmus protuberans* and the cyanobacterium *Oscillatoria agardhii* at three different light supplies. During these experiments, they followed the changes in light absorption of the cultures. In all three cases, *Oscillatoria* competitively excluded *Scenedesmus*. In one of the experiments, *Oscillatoria* was introduced in a *Scenedesmus* culture at steady state. *Oscillatoria* increased, and thereby reduced the light availability to lower levels than the steady-state light availability created by *Scenedesmus*. The decreased light availability was immediately accompanied with a continuous decrease of *Scenedesmus*.

At least qualitatively, these empirical results are in good agreement with our model predictions. However, only a few aspects of our predictions have been tested experimentally yet. Further experiments should reveal to what extent our approach does approximate the behavior of real systems.

Robustness of the model predictions

The assumptions of our model give a rather crude description of light limitation in well-mixed aquatic environments: Lambert-Beer's law provides only an approximation of the underwater light field (Gordon 1989); the Monod equation is one of the simplest ex-

pressions for the relation between light intensity and photosynthesis, but other light-response curves are physiologically more plausible or yield a better fit to the data (Jassby and Platt 1976, Cullen 1990); specific carbon losses need not be constant, but may depend on the light intensity (Weger et al. 1989); the growth rate might depend on the carbon allocation pattern and not be simply proportional to the total carbon gain; and nutrients and light may have interacting effects on phytoplankton growth (Healey 1985).

In spite of these limitations, we think that our model captures at least some essential features of light-limited growth. In fact, with more advanced mathematical techniques, it can be shown that the qualitative results derived in this paper are quite robust (Weissing and Huisman 1994). Our conclusions do not depend on the specific equations used, such as the Monod equation, but on more general assumptions, such as a monotonically increasing light-response curve. Complications arising from photoinhibition (i.e., a nonmonotonic light-response curve) or grazing (i.e., density-dependent losses) can be easily incorporated into our model and will be addressed in a future attempt. Let us here briefly discuss some factors that require more significant changes in the model structure.

The unidirectional flow of light is a crucial assumption underlying our results. In reality, however, photons do not travel in one direction but are frequently scattered within the aquatic medium (Kirk 1983). Although Lambert-Beer's law provides a fairly good approximation in some aquatic environments (Gordon 1989), the angular distribution of the light field can certainly not be neglected in algal mass cultures illuminated from all sides. We do not know whether, in such a "multidirectional" light field, a single critical light intensity is still able to summarize the growth dynamics.

We have neglected the spectral distribution of light and thereby implicitly assumed that all light absorbers utilize light of similar wavelengths. Although this assumption provides a reasonable approximation for many phytoplankton species, it is certainly not always justified. As an extreme example, it is conceivable that purple bacteria and algae stably coexist because purple bacteria utilize infrared light not available to the algae. If spectral aspects are important, wavelength-dependent photosynthesis must be modeled explicitly (Kyewalyanga et al. 1992). One might speculate that the resulting model predictions resemble those of limiting similarity theory, which explicitly deals with partially overlapping resource utilization spectra of competing species (e.g., Abrams 1983).

The equilibrium approach taken in this paper presupposes that the model parameters remain constant. In reality, however, light supply and mixing depth may fluctuate considerably. In addition, the photosynthetic parameters will vary when algae adapt to changes in light availability during vertical mixing (Cullen and Lewis 1988). It is well known that varying conditions promote coexistence of several species on a single resource (Van Gemerden 1974, Powell and Richerson 1985, Sommer 1985, Grover 1990). We therefore expect that our equilibrium predictions are limited to systems where the amplitude of the fluctuations is not too large and the frequency is either large or small when compared to the growth dynamics (cf. Kemp and Mitsch 1979). On the other hand, some of our conclusions have a broader applicability: even in fluctuating environments, a critical light intensity may characterize the conditions that favor phytoplankton growth. Furthermore, the seasonal changes in the light supply lead us to expect seasonal changes in the competitive ability of a species.

Concluding remarks

Our model combines the spatial heterogeneity of a light gradient with a homogeneous distribution of the competitors. We predict competitive exclusion, whereas other studies show that spatial heterogeneity promotes coexistence (e.g., Stephanopoulos and Fredrickson 1979, Ives and May 1985, Smith and Waltman 1991). These studies assume, however, that neither the resource nor the competitors are homogeneously distributed. The assumption that the competitors are not well mixed seems crucial for the argument that spatial heterogeneity promotes coexistence. In our model, competitive exclusion results because "spatial differentiation" of the competitors is prevented. This conclusion lends further support to Hutchinson's (1961) suggestion that turbulent open waters do not allow many opportunities for "niche differentiation," in spite of the spatial heterogeneity caused by a light gradient.

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Literature Cited

Abrams, P. A. 1983. The theory of limiting similarity. Annual Review of Ecology and Systematics **14**:359–376.

Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. American Naturalist **115**:151–170.

Bannister, T. T. 1974. Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. Limnology and Oceanography **19**:1–12.

Butler, G. J., and G. S. K. Wolkowicz. 1985. A mathematical model of the chemostat with a general class of functions describing nutrient uptake. SIAM Journal of Applied Mathematics **45**:138–151.

Butler, G. J., and G. S. K. Wolkowicz. 1987. Exploitative competition in a chemostat for two complementary, and possibly inhibitory, resources. Mathematical Biosciences **83**:1–48.

Cullen, J. J. 1990. On models of growth and photosynthesis in phytoplankton. Deep-Sea Research **37**:667–683.

Cullen, J. J., and M. R. Lewis. 1988. The kinetics of algal photoadaptation in the context of vertical mixing. Journal of Plankton Research **10**:1039–1063.

Dubinsky, Z., P. G. Falkowski, and K. Wyman. 1986. Light harvesting and utilization by phytoplankton. Plant and Cell Physiology **27**:1335–1349.

Evers, E. G. 1991. A model for light-limited continuous cultures: growth, shading, and maintenance. Biotechnology and Bioengineering **38**:254–259.

Fasham, M. J. R., H. W. Ducklow, and S. M. McKelvie. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. Journal of Marine Research **48**: 591–639.

Gieskes, W. W. C., and G. W. Kraay. 1975. The phytoplankton spring bloom in Dutch coastal waters of the North Sea. Netherlands Journal of Sea Research **9**:166–196.

Gordon, H. R. 1989. Can the Lambert-Beer law be applied to the diffuse attenuation coefficient of ocean water? Limnology and Oceanography **34**:1389–1409.

Gran, H. H., and T. Braarud. 1935. A quantitative study of the phytoplankton in the Bay of Fundy and the Gulf of Maine. Journal of the Biological Board of Canada **1**:279–467.

Grover, J. P. 1990. Resource competition in a variable environment: phytoplankton growing according to Monod's model. American Naturalist **136**:771–789.

Hansen, S. R., and S. P. Hubbell. 1980. Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes. Science **207**: 1491–1493.

Healey, F. P. 1985. Interacting effects of light and nutrient limitation on the growth rate of *Synechococcus linearis* (Cyanophyceae). Journal of Phycology **21**:134–146.

Holm, N. P., and D. Armstrong. 1981. Role of nutrient limitation and competition in controlling the populations of *Asterionella formosa* and *Microcystis aeruginosa* in semicontinuous culture. Limnology and Oceanography **26**:622–635.

Hutchinson, G. E. 1961. The paradox of the plankton. American Naturalist **95**:137–145.

———. 1967. A treatise on limnology. II. Introduction to lake biology and the limnoplankton. John Wiley & Sons, New York, New York, USA.

Ives, A. R., and R. M. May. 1985. Competition within and between species in a patchy environment: relations between microscopic and macroscopic models. Journal of Theoretical Biology **115**:65–92.

Jassby, A. D., and T. Platt. 1976. Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. Limnology and Oceanography **21**:540–547.

Kemp, W. M., and W. J. Mitsch. 1979. Turbulence and phytoplankton diversity: a general model of the "paradox of plankton." Ecological Modelling 7:201–222.

Kirk, J. T. O. 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, England.

Kok, B. 1952. On the efficiency of *Chlorella* growth. Acta Botanica Neerlandica **1**:445–467.

Kroon, B. M. A., H. A. M. Ketelaars, H. J. Fallowfield, and L. R. Mur. 1989. Modelling microalgal productivity in a high rate algal pond based on wavelength dependent optical properties. Journal of Applied Phycology **1**:247–256.

Kyewalyanga, M., T. Platt, and S. Sathyendranath. 1992. Ocean primary production calculated by spectral and broadband models. Marine Ecology Progress Series **85**:171–185.

Leon, J. A., and D. Tumpson. 1975. Competition between two species for two complementary or substitutable resources. Journal of Theoretical Biology **50**:185–201.

MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection and character displacement in a patchy environment. Proceedings of the National Academy of Sciences (USA) **51**:1207–1210.

Monsi, M., and T. Saeki. 1953. Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Japanese Journal of Botany **14**:22–52.

Mur, L. R., H. J. Gons, and L. Van Liere. 1977. Some experiments on the competition between green algae and blue-green bacteria in light-limited environments. FEMS Microbiology Letters **1**:335–338.

Phillips, O. M. 1973. The equilibrium and stability of simple marine biological systems. I. Primary nutrient consumers. American Naturalist **107**:73–93.

Platt, T., D. F. Bird, and S. Sathyendranath. 1991. Critical depth and marine primary production. Proceedings of the Royal Society of London, **B 246**:205–217.

Platt, T., and S. Sathyendranath. 1988. Oceanic primary production: estimation by remote sensing at local and regional scales. Science **241**:1613–1620.

Powell, T., and P. J. Richerson. 1985. Temporal variation, spatial heterogeneity, and competition for resources in plankton systems: a theoretical model. American Naturalist **125**:431–464.

Riley, G. A. 1957. Phytoplankton of the North Central Sargasso Sea, 1950–52. Limnology and Oceanography **2**:252–270.

Rothhaupt, K. O. 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. Nature **333**:660–662.

Sakshaug, E., K. Andresen, and D. A. Kiefer. 1989. A steady state description of growth and light absorption in the marine planktonic diatom *Skeletonema costatum*. Limnology and Oceanography **34**:198–205.

Sakshaug, E., and D. Slagstad. 1991. Light and productivity of phytoplankton in polar marine ecosystems: a physiological view. Polar Research **10**:69–85.

Smetacek, V., and U. Passow. 1990. Spring bloom initiation and Sverdrup's critical-depth model. Limnology and Oceanography **35**:228–234.

Smith, H. L., and P. Waltman. 1991. The gradostat: a model of competition along a nutrient gradient. Microbial Ecology **22**:207–226.

Smith, H. V. 1993. Applicability of resource-ratio theory to microbial ecology. Limnology and Oceanography **38**: 239–249.

Smith, R. C., B. B Prézelin, R. R. Bidigare, and K. S. Baker. 1989. Bio-optical modeling of photosynthetic production in coastal waters. Limnology and Oceanography **34**:1524–1544.

Sommer, U. 1985. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. Limnology and Oceanography **30**:335–346.

———. 1989. Nutrient status and nutrient competition of phytoplankton in a shallow, hypertrophic lake. Limnology and Oceanography **34**:1162–1173.

Stephanopoulos, G., and A. G. Fredrickson. 1979. Effect of spatial inhomogeneities on the coexistence of competing microbial populations. Biotechnology and Bioengineering **21**:1491–1498.

Stewart, F. M., and B. R. Levin. 1973. Partitioning of resources and the outcome of interspecific competition: a model and some general considerations. American Naturalist **107**:171–198.

Stockner, J. G. 1968. The ecology of a diatom community in a thermal stream. British Phycological Bulletin **3**:501–514.

Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. Journal du Conseil Permanent International pour l'Exploration de la Mer **18**:287–295.

Taylor, P. A., and P. J. LeB. Williams. 1975. Theoretical studies on the coexistence of competing species under con-

tinuous flow conditions. Canadian Journal of Microbiology **21**:90–98.

Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology **58**:338–348.

———. 1981. Experimental tests of resource competition theory using four species of Lake Michigan algae. Ecology **62**:802–815.

———. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

———. 1985. The resource-ratio hypothesis of plant succession. American Naturalist **125**:827–852.

———. 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. Pages 117–141 *in* J. B. Grace and D. Tilman, editors. Perspectives on plant competition. Academic Press, New York, New York, USA.

Van Gemerden, H. 1974. Coexistence of organisms competing for the same substrate: an example among the purple sulfur bacteria. Microbial Ecology **1**:104–119.

Van Liere, L., and L. R. Mur. 1979. Growth kinetics of *Oscillatoria agardhii* Gomont in continuous culture, limited in its growth by the light energy supply. Journal of General Microbiology **115**:153–160.

Volterra, V. 1928. Variations and fluctuations of the number of individuals in animal species living together. Journal du Conseil Permanent International pour l'Exploration de la Mer **3**:3–51.

Weger H. G., R. Herzig, P. G. Falkowski, and D. H. Turpin. 1989. Respiratory losses in the light in a marine diatom: measurements by short-term mass spectrometry. Limnology and Oceanography **34**:1153–1161.

Weissing, F. J., and J. Huisman. 1994. Growth and competition in a light gradient. Journal of Theoretical Biology, *in press.*

Zevenboom, W., J. van der Does, K. Bruning, and L. R. Mur. 1981. A non-heterocystous mutant of *Aphanizomenon flos-aquae,* selected by competition in light-limited continuous culture. FEMS Microbiology Letters **10**:11–16.

APPENDIX

Here we give a proof of Eq. 19. Taking derivatives with respect to I_{in} on both sides of Eq. 18 yields

$$\frac{p_{max}}{k}\left[\frac{1}{H + I_{in}} - \frac{1}{H + I^*_{out}}\left(e^{kH^*} - kI^*_{out}\frac{dW^*}{dI_{in}}\right)\right] = l\frac{dW^*}{dI_{in}}.$$

Collecting terms containing $\frac{dW^*}{dI_{in}}$ and rearranging yields

$$\frac{1}{kI_{in}}\left(\frac{p_{max}I_{in}}{H + I_{in}} - \frac{p_{max}I_{in}e^{kH^*}}{H + I^*_{out}}\right) = \frac{dW^*}{dI_{in}}\left(l - \frac{p_{max}I^*_{out}}{H + I^*_{out}}\right).$$

In view of Eq. 2 and Eq. 4,

$$\frac{1}{kI_{in}}[p(I_{in}) - p(I^*_{out})] = \frac{dW^*}{dI_{in}}[p(I_c) - p(I^*_{out})],$$

which is equivalent to Eq. 19.