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Growth and Competition in a Light Gradient

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In this paper a general model for growth and competition in a light gradient is developed. The model is based on a few qualitative assumptions: (i) biomass is continuously distributed over depth; (ii) the light gradient is one-dimensional and uni-directional; (iii) photosynthesis is positively related to the local light intensity; and (iv) biomass growth is governed by the carbon balance. By introducing the concept of "quantum return", it is shown that growth can be quantified directly in terms of the light gradient. In monoculture, growth leads to a globally stable equilibrium, at which the light intensity at the bottom of the light gradient is reduced to a "critical light intensity" I^*_{out}. I^*_{out} is not affected by the background turbidity but negatively related to the light supply. When all species are similarly distributed over the light gradient, the outcome of competition can be inferred from this monoculture characteristic: the species with lowest I^*_{out} will competitively exclude all other species. In contrast, spatial differentiation of the competitors may lead to a completely different situation: several species may co-exist, and the species with lowest I^*_{out} may be competitively displaced by species with a better position in the light gradient.

Introduction

Light is a major determinant of the structure and dynamics of terrestrial and aquatic plant communities. While the fundamental importance of light is generally acknowledged, resource competition theory has centered around nutrient-limited growth (reviewed by Tilman, 1982; Waltman, 1990; DeAngelis, 1992). There are, however, two basic differences between nutrients and light. First, light cannot be recycled. Hence a continual influx of light is required for the maintenance of phototrophic growth. Second, 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 created by the competitors themselves.

If species compete for homogeneously distributed nutrients, resource competition theory predicts that:

- The outcome of competition for one nutrient can be inferred from monoculture characteristics: the species that is able to reduce the nutrient concentration to the lowest level (R^*) will competitively exclude all other species.
- The "critical nutrient concentration", R^*, does not depend on the rate at which the nutrient is supplied.
- At equilibrium the number of co-existing species cannot exceed the number of limiting nutrients.

By means of a simple model we could show that similar principles may apply to competition for light in well-mixed aquatic environments (Huisman & Weissing, 1994). Here, the growth dynamics of a species can be characterized by a "critical light intensity" I^*_{out}. I^*_{out} corresponds to the equilibrium light intensity at the bottom of a water column when the species is grown in monoculture. Our model predicts that I^*_{out} plays a similar role for light competition as R^* does for nutrient competition: if light is the only limiting factor, the species with the lowest I^*_{out} competitively excludes all other species. If species are limited by light and one nutrient, at most two species can co-exist in stable equilibrium. In contrast to R^*, however, I^*_{out} is not independent of the resource supply. In fact, I^*_{out} is negatively related to the light supply. As a consequence, the outcome of

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competition for light may depend on the light supply.

The present paper aims at investigating the robustness of these predictions. Our earlier model was based on a number of standard assumptions such as Lambert-Beer's law of light absorption, a Monod equation for carbon uptake and a constant specific carbon loss rate. We intend to show that our main results do not reflect these specific assumptions, but that they can be derived from a couple of fairly general principles.

We extend the scope of our model to terrestrial vegetations and to aquatic environments that are not well mixed. In this context, spatial considerations may become prevalent, since a position on top of the light gradient is inherently advantageous. We are therefore confronted with the question how the outcome of competition is affected by the distribution of the competitors over the light gradient.

Model Structure and Basic Assumptions

The framework for our analysis is depicted in Fig. 1. We focus on a biomass compartment with a cross section of one unit area. A vertical position within this compartment is indicated by its depth s, where s runs from 0 (top) to z (bottom). The biomass compartment is illuminated from above by a constant light supply with intensity I_{in}. The incident light is partly absorbed by biomass. As a consequence, the light intensity I at a certain depth s depends on the amount of biomass $w(s)$ above this depth (Fig. 1). Light that has not been absorbed leaves the compartment with an intensity I_{out}. In a terrestrial system, I_{out} represents the light intensity penetrating through the canopy. In a vessel with algae illuminated from above, I_{out} corresponds to the light intensity leaving the vessel at the bottom.

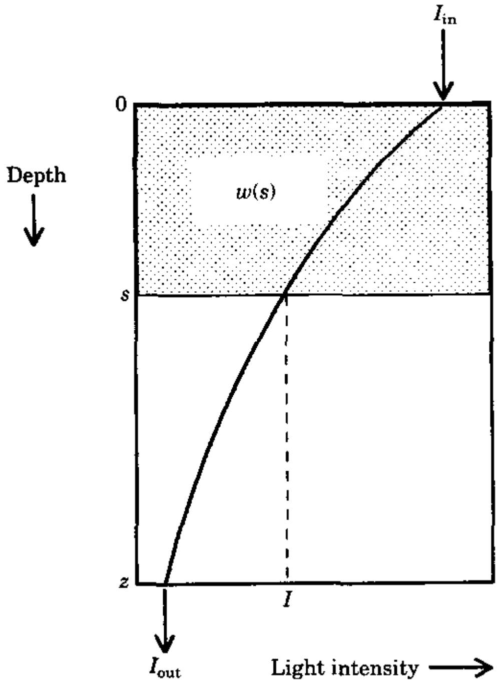

FIG. 1. *Illustration of the model structure: Light with intensity* I_{in} is supplied from above. The light intensity I at depth s results from light absorption by the cumulative biomass $w(s)$ above depth s. Light that has not been absorbed leaves the compartment with an intensity I_{out}.

Under light-limited conditions, biomass growth is governed by the balance between carbon uptake and carbon losses. The difference between carbon uptake and losses will be called the "carbon gain". The carbon gain rate depends on the local light intensity. Owing to shading, the local carbon gain rate varies with depth. Integration of the carbon gain rate over depth yields the total carbon gain rate of the whole biomass compartment. We assume that the total carbon gain rate determines the growth rate of total biomass.

Given the model structure outlined above, we must make assumptions concerning the biomass distribution, the light gradient, the light-dependent carbon gain rate, and the relation between carbon gain and biomass growth.

THE BIOMASS DISTRIBUTION

In our previous paper (Huisman & Weissing, 1994), we dealt with a well-mixed water column. Accordingly, we assumed that biomass was uniformly distributed over depth with density ω. In the present paper, we remove this restriction. We only assume the following:

Assumption 1

The biomass density at depth s, $\omega(s)$, is given by a continuous function ω of depth.

Although the continuity of ω is mainly a technical requirement, it excludes the possibility that the complete biomass gets concentrated in an infinitely thin layer on top of the light gradient. In an infinitely thin biomass layer, shading might become negligible. In practice, however, such extreme biomass concentrations seldom occur.

The light availability at a given depth depends on the light intercepted by the biomass *above* this depth. The "cumulative biomass" above depth s, $w(s)$, is given by

$$w(s) = \int_0^s \omega(\sigma)\,d\sigma. \tag{1}$$

Notice that the biomass density at depth s can be expressed as the change of cumulative biomass with depth:

$$\frac{dw}{ds} = \omega(s). \tag{2}$$

The total biomass in the whole compartment will be denoted by W:

$$W = w(z) = \int_0^z \omega(s)\,ds. \tag{3}$$

LIGHT ABSORPTION

Our previous model assumed that light absorption is governed by Lambert-Beer's law. Accordingly, the light intensity I below a cumulative biomass w was given by

$$I(w) = I_{in}\,e^{-kw}, \tag{4}$$

where I_{in} is the incident light and k is the light extinction coefficient of biomass. Although Lambert-Beer's law is a rather standard assumption, it provides at best an approximation of underwater light fields (Kirk, 1983; Gordon, 1989) or the light availability in terrestrial vegetations (Monsi & Saeki, 1953; Thornley & Johnson, 1990). In the present paper, we use a more general description of the light gradient that includes alternative formulations of light availability such as the light absorption function proposed by Reynolds & Pacala (1993):

$$I(w) = \frac{I_{in}}{1 + kw}. \tag{5}$$

Assumption 2.1.

The light intensity I at a certain depth is a continuously differentiable function φ of the light supply I_{in} and the product of the light extinction coefficient k and the cumulative biomass w above this depth:

$$I(w) = \varphi(I_{in}, kw). \tag{6}$$

I is positively related to the light supply (i.e. $\partial\varphi/\partial I_{in} > 0$) and negatively related to cumulative biomass (i.e. $\partial\varphi/\partial(kw) < 0$).

As indicated by eqn (6), I_{in} and k are viewed as parameters, whereas w is considered a variable. The inclusion of the light extinction coefficient in the formalism makes the treatment of growth in a monoculture a bit more cumbersome, but it will be useful in the context of competition.

In view of the interpretation of I_{in}, the function φ has to satisfy the compatibility requirement:

$$I_{in} = I(0) = \varphi(I_{in}, 0). \tag{7}$$

The light intensity at the bottom of the biomass compartment,

$$I_{out} = I(W) = \varphi(I_{in}, kW), \tag{8}$$

is a function of total biomass. Since I is negatively related to biomass, I_{out} decreases with increasing total biomass:

$$\frac{dI_{out}}{dW} < 0. \tag{9}$$

In addition to Assumption 2.1, we postulate that the incident light is completely absorbed if total biomass tends to infinity:

$$\lim_{W\to\infty} I_{out} = 0. \tag{10}$$

Notice that our model does not specify any particular light absorption function. Accordingly, Assumption 2.1 might also apply to other resource gradients generated by biomass. Water-limited growth in a vertical soil moisture gradient might be an example.

A UNI-DIRECTIONAL LIGHT FLUX

We make an additional assumption on the light gradient which is not really essential, but which simplifies the analysis considerably. Basically, we assume that the light flux is "uni-directional".

Imagine that a certain amount of biomass w is split into two parts, $w = u + v$, where u is located on top of v (see Fig. 2). If light flows in one direction, the incident light intensity I_{in} is first reduced by u to the level $I(u) = \varphi(I_{in}, ku)$. Subsequently, the light intensity $I(u)$ is further reduced by v to the level $I(u + v) = \varphi(I(u), kv)$. On the other hand, light reduction by the combined biomass $u + v$ is given by $I(u + v) = \varphi(I_{in}, k(u + v))$. Thus, we are led to:

Assumption 2.2.

The light flux is uni-directional, i.e. the function φ has the property:

$$\varphi(I_{in}, k(u + v)) = \varphi(\varphi(I_{in}, ku), kv). \tag{11}$$

In essence, Assumption 2.2 states that the light supply for v only depends on the light intensity that leaves u, and not directly on the amount u itself. The most important consequence of this assumption is that light absorption per unit biomass, dI/dw, only depends on the local light intensity I and that it can be written in the form

$$\frac{dI}{dw} = -ka(I), \tag{12}$$

where a is a positive function of the light intensity I. This result is derived in Appendix A.

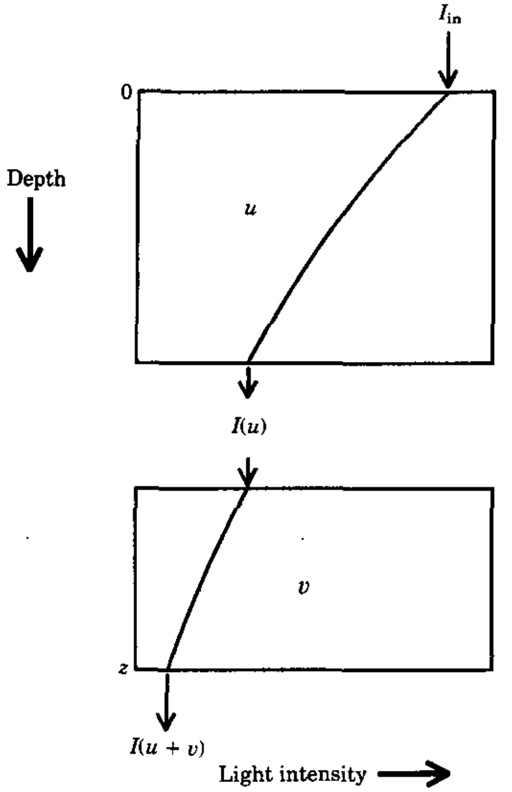

FIG. 2. The light flux through two consecutive biomass compartments, u and v. If the light flux is uni-directional, the light intensity $I(u)$ left by u provides the light supply for v. Hence, the light intensity at the bottom of the light gradient is given by $I(u+v) = \varphi(I(u), kv)$.

Lambert-Beer's law is, of course, the most prominent example describing a uni-directional light flux:

$$I(u+v) = I_{in}\,e^{-k(u+v)} = I_{in}\,e^{-ku}\,e^{-kv} = I(u)e^{-kv}.$$

But Assumption 2.2 also includes other functions, for example, Monteith's (1965) binomial light absorption model and the linear expression $I = I_{in} - kw$. The latter is probably not a good description of a light gradient, but it might well describe other resource gradients generated by biomass. Assumption 2.2 does not apply to the light absorption function (5) considered by Reynolds & Pacala (1993). However, even this function can be included in our formalism (see Appendix B).

THE CARBON BALANCE

The specific (= per unit biomass) carbon gain rate, g, is defined as the difference between the specific carbon uptake rate and the specific carbon loss rate. In our previous paper, the dependence of specific carbon uptake on light intensity was described by a Monod equation, while specific carbon losses, ℓ, were assumed to be constant:

$$g(I) = p_{max}\frac{I}{H+I} - \ell. \qquad (13)$$

Although the Monod equation is one of the simplest expressions for the relation between light intensity and photosynthesis, other light-response curves are physiologically more plausible (Marshall & Biscoe, 1980; Sakshaug *et al.*, 1989) or yield a better fit to the data (Jassby & Platt, 1976). Furthermore, the photosynthetic parameters need not be constant over depth, but may adapt to the local light availability (e.g. Cullen & Lewis, 1988). The assumption that the specific carbon loss rate is constant may also be unrealistic. Losses due to photorespiration, for example, are directly coupled to photosynthesis and may therefore depend on light intensity. Carbon losses will also be light-dependent in the context of carbon allocation: If we assume that a fraction A of the specific carbon uptake rate $p(I)$ is allocated to *non-photosynthetic tissues*, the losses due to allocation become a function of local light intensity: $\ell(I) = Ap(I)$.

In the present paper, we do not specify an explicit carbon uptake or loss function. We only assume the following (see Fig. 3):

Assumption 3

The specific carbon gain rate, $g(I)$, is given by a monotonically increasing function g of the light intensity:

$$\frac{dg}{dI} > 0. \qquad (14)$$

The specific carbon gain rate is negative if no light is available:

$$g(0) < 0. \qquad (15)$$

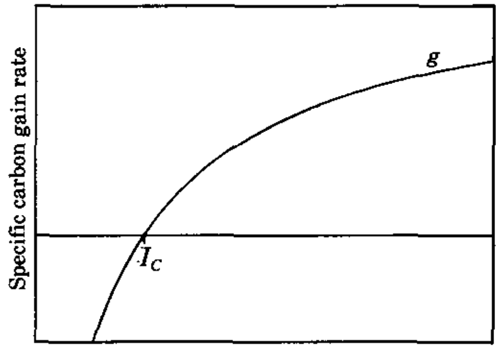

FIG. 3. The specific carbon gain rate g as an increasing function of the light intensity I (Assumption 3). By definition, g is zero at the compensation point I_C.

Assumption 3 applies to almost all light response curves proposed in the literature. However, it does not include photo-inhibition where the carbon gain rate decreases at high light intensities. Yet, the monotonicity assumption is not really crucial. In contrast, the assumption that the specific carbon gain *only* depends on the local light availability is essential for our modeling approach. We shall return to this point in the discussion.

The light intensity at which the specific carbon uptake is exactly balanced by the specific carbon losses is defined as the "compensation point" I_C (Fig. 3):

$$g(I_C)=0. \tag{16}$$

Notice that the compensation point is independent of the light supply I_{in} since g is, by assumption, independent of I_{in}.

The "local carbon gain rate" at depth s is given by the product $g(I(s))\omega(s)$ of the specific carbon gain rate at depth s and the biomass density at depth s. The "total carbon gain rate" G is obtained by integrating the local carbon gain rate over all depths:

$$G=\int_0^z g(I(w(s)))\omega(s)\,\mathrm{d}s. \tag{17}$$

The notation $g(I(w(s)))$ illustrates the nested structure of the model, where g depends on I, I depends on w, and w depends on s.

THE GROWTH DYNAMICS

In our previous model, we assumed that the change in total biomass is proportional to the total carbon gain rate:

$$\frac{\mathrm{d}W}{\mathrm{d}t}=\alpha G. \tag{18}$$

In general, growth may be linked to carbon gain in a nonlinear way:

Assumption 4

The change in total biomass is positively related to the total carbon gain rate:

$$\frac{\mathrm{d}W}{\mathrm{d}t}=F(G), \tag{19}$$

where F is a strictly increasing function of G. There is no growth if the total carbon gain is zero, i.e. $F(0)=0$.

Notice that Assumption 4 formulates the dynamics of *total* biomass in terms of the *total* carbon gain rate. Since photosynthesis takes place at a local level, it might be more plausible to focus on the *local* biomass density $\omega(s,t)$ at depth s and time t. We now justify Assumption 4 on the basis of such local considerations. In our previous model, eqn (19) was simply the consequence of complete mixing. Without complete mixing, there are several ways to derive Assumption 4 from the local biomass dynamics $\partial\omega/\partial t$. In particular, we have two scenarios in mind:

(i) Consider an even-aged stand of highly integrated plants where each individual has its leaves distributed over the whole light gradient. Suppose that local growth is governed by allocation decisions taken by the whole plant on basis of its total carbon gain. In this case, we may assume that the change in local biomass density is a function of the total carbon gain rate and the position of a leaf in the light gradient:

$$\frac{\partial\omega}{\partial t}(s,t)=f(G,s). \tag{20}$$

In view of (3), we immediately arrive at Assumption 4:

$$\frac{\mathrm{d}W}{\mathrm{d}t}=\int_0^z\frac{\partial\omega}{\partial t}(s,t)\,\mathrm{d}s=\int_0^z f(G,s)\,\mathrm{d}s=F(G).$$

In fact, many models simulating agricultural crop growth are implicitly based on these kinds of arguments (cf. Thornley & Johnson, 1990).

(ii) Alternatively, consider a large phytoplankton population where growth is fully governed by local processes. In this scenario, the local dynamics will be determined by the local carbon gain rate and, in addition, by the displacement of phytoplankton cells due to transport processes. Now the change in local biomass density can be described by a partial differential equation:

$$\frac{\partial\omega}{\partial t}(s,t)=\alpha g(I(s,t))\omega(s,t)-\frac{\partial J}{\partial s}(s,t), \tag{21}$$

where the first term, $\alpha g(I)\omega$, represents local growth whereas the second term, $-\partial J/\partial s$, represents local transport processes. The "flux" $J(s,t)$ corresponds to the number of phytoplankton cells crossing a horizontal section of the compartment at depth s. Examples for such a flux include diffusion, convection, and migration (e.g. Edelstein-Keshet, 1988). If the compartment is closed, no cells can enter or leave the compartment at the boundaries:

$$J(0,t)=J(z,t)=0.$$

Together with these boundary conditions, the local growth dynamics (21) again leads to Assumption 4:

$$\begin{aligned}\frac{\mathrm{d}W}{\mathrm{d}t}&=\int_0^z\frac{\partial\omega}{\partial t}(s,t)\,\mathrm{d}s\\&=\alpha\int_0^z g(I(s,t))\omega(s,t)\,\mathrm{d}s-\int_0^z\frac{\partial J}{\partial s}(s,t)\,\mathrm{d}s\end{aligned}$$

$$= \alpha G - [J(z,t) - J(0,t)]$$
$$= \alpha G.$$

Growth in Monoculture

In this section, we investigate the implications of Assumptions 1–4 for light-limited growth in a monoculture. Notice that we implicitly assume that light is only absorbed by biomass (Assumption 2.1). Of course, in reality, light is also absorbed by other substances such as water, detritus, or litter. In the next section, these inanimate light absorbers will be included in our formalism (see Result 7).

TOTAL CARBON GAIN AND TOTAL BIOMASS

The total carbon gain rate G has been defined in terms of the biomass distribution $\omega(s)$. Substituting (2) into (17), we obtain:

$$G = \int_0^z g(I(w(s)))\frac{\mathrm{d}w}{\mathrm{d}s}\,\mathrm{d}s.$$

Hence, G may be viewed as a function of total biomass:

$$G(W) = \int_0^W g(I(w))\,\mathrm{d}w. \tag{22}$$

G has the following properties (see Fig. 4):

Result 1

The total carbon gain rate G is a concave function of total biomass. G is maximal if the light intensity at the bottom of the light gradient equals the compensation point. With increasing total biomass, G becomes negative.

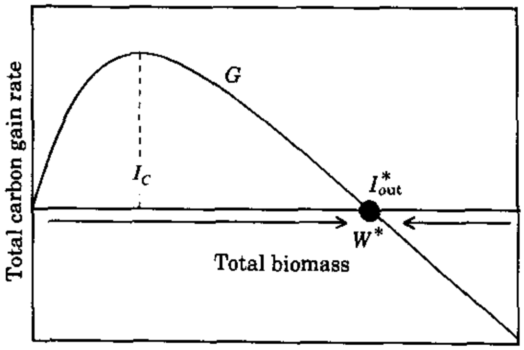

FIG. 4. The total carbon gain rate G as a function of total biomass. G is zero at the globally stable equilibrium W^*. G is also illustrated in terms of the light intensity I_{out} at the bottom of the light gradient. I_{out} decreases from left to right. G is maximal at $I_{out} = I_C$ and G is zero at $I_{out} = I^*_{out}$.

In order to prove this result note that, in view of (22), the derivative of G with respect to W is given by:

$$\frac{\mathrm{d}G}{\mathrm{d}W} = g(I(W)) = g(I_{out}). \tag{23}$$

In other words, the change of total carbon gain with total biomass corresponds to the specific carbon gain rate at the bottom of the light gradient. As a consequence, G is increasing with total biomass for $g(I_{out}) > 0$ and decreasing for $g(I_{out}) < 0$. Hence, G is maximal for $g(I_{out}) = 0$. In view of (16), this maximum corresponds to $I_{out} = I_C$.

The second derivative of G with respect to W is negative:

$$\frac{\mathrm{d}^2G}{\mathrm{d}W^2} = \frac{\mathrm{d}}{\mathrm{d}W}g(I_{out}) = \frac{\mathrm{d}g}{\mathrm{d}I}\frac{\mathrm{d}I_{out}}{\mathrm{d}W} < 0.$$

Thus, the total carbon gain rate is a concave function of total biomass. Furthermore, in view of (10) and (15), G will decrease with W when total biomass becomes large, i.e.

$$\lim_{W\to\infty}\frac{\mathrm{d}G}{\mathrm{d}W} = \lim_{W\to\infty} g(I_{out}) < 0.$$

Since G is concave, G will decrease beyond all bounds:

$$\lim_{W\to\infty} G(W) = -\infty. \qquad \square$$

TOTAL CARBON GAIN AND THE LIGHT GRADIENT

Up to now, the total carbon gain rate has been viewed as an integral over depth [eqn (17)], or as an integral over cumulative biomass [eqn (22)]. These representations reflect two prominent approaches in aquatic and terrestrial ecology, respectively. Integration over depth is often used in models of algal photosynthesis (e.g. Sverdrup, 1953; Kirk, 1983), while integration over cumulative biomass is commonly used in models of plant canopy photosynthesis (e.g. Monsi & Saeki, 1953; Johnson & Thornley, 1984). Here we outline a third approach. We argue that a better intuitive understanding of light-limited growth can be obtained if the total carbon gain rate is not interpreted in terms of depth or biomass but directly in terms of the light gradient.

If light absorption is governed by Lambert-Beer's law, such an approach is straightforward (Johnson *et al.*, 1989; Huisman & Weissing, 1994), because light absorption per unit biomass is proportional to the local light intensity:

$$\frac{\mathrm{d}I}{\mathrm{d}w} = -kI.$$

As a consequence, the total carbon gain rate can be written as an integral over light intensity:

$$G = \int_0^W g(I(w))\,\mathrm{d}w = \int_0^W \frac{g(I(w))}{-kI(w)}\frac{\mathrm{d}I}{\mathrm{d}w}\,\mathrm{d}w$$

$$= \int_{I_{\text{out}}}^{I_{\text{in}}} \frac{g(I)}{kI}\,\mathrm{d}I. \qquad (24)$$

The minus sign is accomodated by exchanging the integration boundaries. The integrand in (24), $g(I)/kI$, has been called the "quantum return" (Huisman & Weissing, 1994). It corresponds to the carbon gain per unit biomass divided by the light absorption per unit biomass. Hence, the quantum return has a clear-cut physiological interpretation: it is the carbon gain per unit of light (i.e. per quantum) absorbed.

We now show how this approach extends to our general framework. In general, we define the "quantum return" as

$$q = \frac{g(I)}{-\mathrm{d}I/\mathrm{d}w}.$$

In view of (12), the quantum return only depends on the local light intensity I:

$$q(I) = \frac{g(I)}{ka(I)}. \qquad (25)$$

Hence the total carbon gain rate can be written as:

$$G = \int_0^W g(I(w))\,\mathrm{d}w = \int_0^W \frac{g(I(w))}{\mathrm{d}I/\mathrm{d}w}\frac{\mathrm{d}I}{\mathrm{d}w}\,\mathrm{d}w$$

$$= \int_{I_{\text{out}}}^{I_{\text{in}}} q(I)\,\mathrm{d}I.$$

Result 2

In a uni-directional light flux, the total carbon gain rate can be represented as an integral of quantum return over the light gradient. Therefore G can be viewed as a function of I_{out}:

$$G(I_{\text{out}}) = \int_{I_{\text{out}}}^{I_{\text{in}}} q(I)\,\mathrm{d}I. \qquad (26)$$

The quantum return, q, only depends on the local light intensity. $q(I)$ is positive for $I > I_C$, and negative for $I < I_C$.

The properties of the function G derived above (see Fig. 4) become transparent if the integral (26) is split into two terms:

$$G(I_{\text{out}}) = \int_{I_C}^{I_{\text{in}}} q(I)\,\mathrm{d}I + \int_{I_{\text{out}}}^{I_C} q(I)\,\mathrm{d}I. \qquad (27)$$

If $I_{\text{in}} > I_C > I_{\text{out}}$, the first term corresponds to the part of the light gradient where the quantum return is positive, while the second term corresponds to light intensities where the quantum return is negative. Hence eqn (27) shows again that $G(I_{\text{out}})$ is decreasing for $I_{\text{out}} < I_C$, and that the total carbon gain is maximal for $I_{\text{out}} = I_C$.

THE DYNAMICS OF LIGHT LIMITED GROWTH

Assumption 4 implies that total biomass will grow if the total carbon gain is positive and that it will decay if total carbon gain is negative. It is obvious that growth is only possible if the light supply exceeds the compensation point. We therefore assume that $I_{\text{in}} > I_C$. In this case, the total carbon gain rate is positive for low biomass and negative for high biomass (Fig. 4). Since G is concave with respect to total biomass, there is a unique nontrivial intersection point with the W-axis:

$$G(W^*) = 0, \quad \text{or equivalently,} \quad G(I^*_{\text{out}}) = 0. \qquad (28)$$

In view of Assumption 4, W^* is an equilibrium of the biomass dynamics. This equilibrium is globally stable since total carbon gain is positive when total biomass is below W^* and negative when above W^*. In view of (28), the equilibrium is characterized by the light intensity I^*_{out} at the bottom of the light gradient. I^*_{out} is a "critical light intensity" since biomass will increase if $I_{\text{out}} > I^*_{\text{out}}$ and decrease if $I_{\text{out}} < I^*_{\text{out}}$.

Notice that the positive and the negative term in eqn (27) exactly balance in equilibrium. As a consequence, I^*_{out} is always smaller than I_C (see Fig. 4). Summarizing, we have shown:

Result 3

Total biomass can only grow if the light supply exceeds the compensation point. If I_{in} exceeds I_C, a globally stable biomass equilibrium W^* will be reached. At this equilibrium,

$$I_{\text{in}} > I_C > I^*_{\text{out}}. \qquad (29)$$

Thus, the light intensity at the bottom of the light gradient is reduced beyond the compensation point.

Notice that the equilibrium of total biomass does not reflect steady state conditions at the local level. In the top of the light gradient, above the compensation point, the carbon gain is always positive. On the other hand, carbon losses exceed carbon uptake at the bottom of the light gradient. It is the balance between these non-equilibrium processes at the local level that leads to a steady state of the total biomass.

DEPENDENCE ON THE LIGHT SUPPLY

We now investigate the dependence of the equilibrium characteristics on the light supply. We shall show

Result 4

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

It is not surprising that the equilibrium biomass is positively related to I_{in}. In fact, W^* is given by the equilibrium equation

$$G(I_{\text{in}}, W^*) = \int_0^{W^*} g(\varphi(I_{\text{in}}, kw))\,\mathrm{d}w = 0, \qquad (30)$$

where the notation makes the dependence of G on I_{in} explicit. Implicit differentiation of eqn (30) yields

$$\frac{\partial G}{\partial I_{\text{in}}}(I_{in}, W^*) + \frac{\partial G}{\partial W}(I_{in}, W^*)\frac{\mathrm{d}W^*}{\mathrm{d}I_{\text{in}}} = 0,$$

which leads to

$$\frac{\mathrm{d}W^*}{\mathrm{d}I_{\text{in}}} = -\frac{\dfrac{\partial G}{\partial I_{\text{in}}}(I_{\text{in}}, W^*)}{\dfrac{\partial G}{\partial W}(I_{\text{in}}, W^*)}. \qquad (31)$$

The numerator in (31) is positive since the integrand of (30), $g(\varphi(I_{\text{in}}, kw))$, is positively related to I_{in}. The denominator corresponds to the slope of the function G with respect to W, which is negative in W^* (see Fig. 4). Hence $\mathrm{d}W^*/\mathrm{d}I_{\text{in}}$ is indeed positive.

It is perhaps more surprising that the sign of the relationship between I^*_{out} and I_{in} can be inferred from our general assumptions. We write the equilibrium equation $G(I^*_{\text{out}}) = 0$ in the form (27) in order to make the dependence of I^*_{out} on I_{in} more explicit:

$$G(I_{\text{in}}, I^*_{\text{out}}) = \int_{I_C}^{I_{\text{in}}} q(I)\,\mathrm{d}I + \int_{I^*_{\text{out}}}^{I_C} q(I)\,\mathrm{d}I = 0. \qquad (32)$$

Implicit differentiation of this equation with respect to I_{in} yields

$$q(I_{\text{in}}) - q(I^*_{\text{out}})\frac{\mathrm{d}I^*_{\text{out}}}{\mathrm{d}I_{\text{in}}} = 0,$$

which leads to

$$\frac{\mathrm{d}I^*_{\text{out}}}{\mathrm{d}I_{\text{in}}} = \frac{q(I_{\text{in}})}{q(I^*_{\text{out}})}. \qquad (33)$$

Now it is obvious that I^*_{out} is negatively related to I_{in}, since $q(I_{\text{in}}) > 0$ and $q(I^*_{\text{out}}) < 0$.

A closer look at eqn (32) reveals the intuition behind Result 4: an increase of the light supply I_{in} leads to an increase of the total quantum return above the compensation point (the first integral in (32)]. At equilibrium, the increased positive quantum return above I_C must be balanced by an increased negative quantum return below I_C. This is only possible if the second integral in (32) becomes more negative, i.e. if the light gradient below I_C is extended to a lower light intensity I^*_{out}.

Competition for Light

We have thus far assumed that light is only absorbed by the biomass of a single species. Since this species generated its own light regime, depth became a dummy variable. Accordingly, it was not necessary to specify the distribution of biomass over depth. In this section, we introduce other light absorbers like water, detritus, and competing species. Now the relative positions of the species in the light gradient become important since a species growing on top of the gradient has an enormous positional advantage.

The present paper does not address the question how the biomass distributions over depth are generated. Instead, we consider the relative positions of the competing species as given and focus on the question how a given positional relation affects the outcome of competition. First, we investigate competition in the absence of spatial differentiation, i.e. the situation where all species have a similar distribution over the light gradient. This scenario will be contrasted with a situation where some species have a positional advantage over their competitors.

BASIC ASSUMPTIONS

We assume that light-limited growth in a mixture is governed by similar principles as light-limited growth in monoculture. We consider a number of light absorbers which are indicated by the subscripts i and j. For inanimate light absorbers (e.g. water or litter), we assume that the specific carbon gain rate is zero, i.e. they neither grow nor decay. For each living species i, g_i is again a monotonic function of the local light intensity I, and its total carbon gain rate is still given by:

$$G_i = \int_0^z g_i(I(s))\omega_i(s)\,\mathrm{d}s. \qquad (34)$$

We still assume that the change in total biomass of species i is governed by its total carbon gain rate:

$$\frac{\mathrm{d}W_i}{\mathrm{d}t} = F_i(G_i), \qquad (35)$$

where F_i is an increasing function of G_i, and $F_i(0) = 0$. This formulation implies that the growth rates of the competing species only depend on the light availability. In other words, there is no direct interference, there are no toxic interactions, and growth is not limited by other resources. The species only interact via shading. Mutual shading is again characterized by a light absorption function φ:

Assumption 2′

The light intensity I at depth s is a positive function φ of the light supply I_{in} and the cumulative amounts $w_j(s)$ of all light absorbers above depth s:

$$I(s) = \varphi(I_{\text{in}}, \sum_j k_j w_j(s)), \tag{36}$$

where k_j is the light extinction coefficient of light absorber j. As before (Assumption 2), the function φ is increasing in its first component, decreasing in its second component, and it describes a uni-directional light flow.

COMPETITION IN THE ABSENCE OF SPATIAL DIFFERENTIATION

Parallel distributions

In this section, we assume that there is no spatial differentiation, i.e. that all light absorbers have a similar distribution over depth. More formally, two light absorbers i and j are said to be "distributed in parallel" if the ratio of their local densities, $\omega_i(s)/\omega_j(s)$, is the same at all depths. If two light absorbers are distributed in parallel, the ratio of their local densities is reflected by the ratio of their total biomass:

$$\frac{\omega_i(s)}{\omega_j(s)} = \frac{w_i(s)}{w_j(s)} = \frac{W_i}{W_j} \quad \text{for all} \quad s. \tag{37}$$

The shape of the distribution ω_i can be characterized by the relative distribution $\omega_i(s)/W_i$. If all light absorbers are distributed in parallel, these relative distributions are identical. The common relative distribution will be denoted by ρ:

$$\rho(s) = \frac{\omega_i(s)}{W_i} \quad \text{for all} \quad i. \tag{38}$$

As a consequence, the relative cumulative biomasses, $w_i(s)/W_i$, are also identical and given by the integral:

$$r(s) = \int_0^s \rho(\sigma)\,\mathrm{d}\sigma = \frac{w_i(s)}{W_i} \quad \text{for all} \quad i.$$

We say that there is no "spatial differentiation" if all light absorbers are distributed in parallel or, equivalently, if their relative biomass distributions are identical.

Partitioning of the light gradient

In the absence of spatial differentiation, light absorption in a mixture is very similar to light absorption in a monoculture. In fact, the light gradient can be written in terms of the common relative distribution r:

$$I = \varphi(I_{\text{in}}, \sum k_j w_j) = \varphi(I_{\text{in}}, \kappa r), \tag{39}$$

where

$$\kappa = \sum k_j W_j \tag{40}$$

is a measure for total light absorption. Formally, the light gradient (39) corresponds to a gradient induced by a single species with cumulative biomass $r(s)$ and (time-dependent) light extinction κ. This correspondence has important implications:

Result 5

In the absence of spatial differentiation, the total carbon gain rate of species i in mixture, $G_{i,\text{mix}}$, can be expressed in terms of the quantum return of species i:

$$G_{i,\text{mix}} = \frac{k_i W_i}{\sum k_j W_j} \int_{I_{\text{out}}}^{I_{\text{in}}} q_i(I)\,\mathrm{d}I. \tag{41}$$

Equation (41) 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,

$$G_{i,\text{mono}} = \int_{I_{\text{out}}}^{I_{\text{in}}} q_i(I)\,\mathrm{d}I, \tag{42}$$

corresponds to the total carbon gain that species i would have obtained in the same light gradient when grown in monoculture. Thus (41) just states which fraction of the total light absorption is available for the carbon gain of species i.

In order to prove Result 5, we shall apply eqn (12) to the light gradient described by (39). In view of $\mathrm{d}r/\mathrm{d}s = \rho(s)$, we obtain:

$$\frac{\mathrm{d}I}{\mathrm{d}s} = \frac{\mathrm{d}I}{\mathrm{d}r}\frac{\mathrm{d}r}{\mathrm{d}s} = -\kappa a(I)\rho(s).$$

As a consequence, the total carbon gain rate (34) can be written as an integral over light intensity:

$$G_{i,\text{mix}} = \int_0^z \frac{g_i(I)\omega_i(s)}{-\kappa a(I)\rho(s)}\frac{\mathrm{d}I}{\mathrm{d}s}\,\mathrm{d}s = \int_{I_{\text{out}}}^{I_{\text{in}}} \frac{g_i(I)W_i}{\kappa a(I)}\,\mathrm{d}I.$$

Using the definition of quantum return [eqn (25)], this reduces to:

$$G_{i,\text{mix}} = \frac{k_i W_i}{\kappa} \int_{I_{\text{out}}}^{I_{\text{in}}} \frac{g_i(I)}{k_i a(I)}\,\mathrm{d}I = \frac{k_i W_i}{\sum k_j W_j} \int_{I_{\text{out}}}^{I_{\text{in}}} q_i(I)\,\mathrm{d}I. \qquad \square$$

Light requirements for growth

Species i will increase if its total carbon gain in mixture, $G_{i,\mathrm{mix}}$, is positive. Result 5 implies that $G_{i,\mathrm{mix}}$ has the same sign as the total carbon gain rate in monoculture, $G_{i,\mathrm{mono}}$. We have already seen that the sign of $G_{i,\mathrm{mono}}$ is determined by the critical light intensity $I^*_{\mathrm{out},i}$ of species i: $G_{i,\mathrm{mono}}$ is positive if and only if the light intensity at the bottom of the light gradient exceeds $I^*_{\mathrm{out},i}$. Hence, we obtain

Result 6

In the absence of spatial differentiation, the critical light intensity of species i in monoculture specifies when this species will grow in mixture: Species i will increase if $I_{\mathrm{out}} > I^*_{\mathrm{out},i}$, it will decrease if $I_{\mathrm{out}} < I^*_{\mathrm{out},i}$, and it will remain stationary if $I_{\mathrm{out}} = I^*_{\mathrm{out},i}$.

This result has also implications for growth in monoculture. When talking about a monoculture of species i, we have thus far assumed that light is only absorbed by the species itself. In practice, light is also absorbed by other substances like water or detritus. Suppose that, in the absence of species i, these inanimate light absorbers would reduce the light intensity at the bottom of the light gradient to the "background level" $I_{\mathrm{out,bg}}$. In view of Result 6, species i will only be able to grow in mixture with these light absorbers if the background level exceeds its critical light intensity $I^*_{\mathrm{out},i}$. If $I_{\mathrm{out,bg}} > I^*_{\mathrm{out},i}$, species i will grow until it has reduced the light availability at the bottom of the light gradient to its critical light intensity:

Result 7

In the presence of inanimate light absorbers, distributed in parallel, a monoculture of species i will reduce I_{out} to the same critical light intensity $I^*_{\mathrm{out},i}$ as in the absence of these light absorbers.

Competitive exclusion

Result 6 provides the key for understanding competition for light in the absence of spatial differentiation. First, Result 6 implies that several species can only coexist in equilibrium if they have identical critical light intensities. Such a situation is rather unlikely and structurally unstable. Hence, the possibility of equilibrium co-existence can be neglected. Second, Result 6 shows that the species with the lowest critical light intensity can always invade the monoculture of any other species. On the other hand, no other species can invade the monoculture of the species with lowest I^*_{out}. Accordingly, there is exactly one stable equilibrium, the monoculture of the species with lowest I^*_{out}. In Appendix C, it is shown that this equilibrium is globally stable. In other words, light absorption is maximized by competition for light:

Result 8

In the absence of spatial differentiation, the species with the lowest critical light intensity I^*_{out} will competitively exclude all other species. Since I^*_{out} depends on I_{in}, the outcome of competition may depend on the light supply.

COMPETITION IN THE PRESENCE OF SPATIAL DIFFERENTIATION

Up to now, we have assumed that all species have a similar distribution over the light gradient. In most aquatic and terrestrial systems, however, the relative positions of the competitors are at least partly determined by processes such as differential growth, allocation, phototropism, or dispersal. These processes typically lead to spatial differentiation of the competitors. In this paper, we do not investigate how spatial differentiation develops. But by means of a simple example we can illustrate that, in the presence of spatial differentiation, the position of a species in the light gradient may become prevalent:

Result 9

In the presence of spatial differentiation:

(i) Equilibrium co-existence of several species may occur.
(ii) Co-existence may depend on the light supply.
(iii) The species with lowest critical light intensity may be competitively excluded by species with better positions in the light gradient.

In order to prove Result 9, we examine the most extreme form of spatial differentiation. Consider two species where species 1 grows completely above species 2. One might think of a phytoplankton species under a canopy of floating water plants, or of mosses and ferns on a forest floor. We assume that the light supply I_{in} exceeds the compensation point $I_{C,1}$ of species 1. Species 1 is not affected by species 2. Hence, species 1 will grow until its monoculture equilibrium is reached. At this equilibrium, the light intensity penetrating through the biomass of species 1 is given by $I^*_{\mathrm{out},1}$. The light intensity $I^*_{\mathrm{out},1}$ provides the light supply for species 2. As a consequence (see Result 3), species 2 is able to grow whenever:

$$I^*_{\mathrm{out},1} > I_{C,2}. \tag{43}$$

Hence, the two species will stably co-exist if the compensation point of species 2 is low enough to satisfy this condition. Analogously, n species will co-exist in n distinct layers if $I^*_{\mathrm{out},i} > I_{C,i+1}$ for all i.

In view of Result 4, $I^*_{\mathrm{out},1}$ is negatively related to I_{in}. On the other hand, $I_{C,2}$ is independent of I_{in}. Hence, it is conceivable that (43) is satisfied at a low I_{in}, while it is not satisfied at a high I_{in}. In this simple scenario at least, the likelihood of co-existence is reduced by an increase of the light supply.

According to Result 3, the critical light intensity of species 2 (as measured in monoculture) is lower than its compensation point: $I_{C,2} > I^*_{out,2}$. For this reason, it is easy to construct specific examples where the critical light intensity of species 1 falls between the compensation point and the critical light intensity of species 2:

$$I_{C,2} > I^*_{out,1} > I^*_{out,2}. \qquad (44)$$

In this case, (43) is not satisfied and species 2 is not able to grow in the shade of species 1. This demonstrates that the species with lowest I^*_{out} may be competitively excluded by a species with a better position in the light gradient. In other words, the superior light competitor in the absence of spatial differentiation can be competitively displaced in the presence of spatial differentiation.

Discussion

ROBUSTNESS OF THE MODEL PREDICTIONS

Recently, we investigated a simple model for light-limited growth and competition among phytoplankton species in a well-mixed aquatic environment (Huisman & Weissing, 1994). This model was based on a few standard assumptions:

- a uniform biomass distribution;
- a light gradient described by Lambert-Beer's law;
- a Monod equation for carbon uptake and a constant specific carbon loss rate;
- a linear relation between biomass growth and total carbon gain.

A number of testable predictions were derived from these assumptions: (i) The light requirements of a phytoplankton species can be characterized by its critical light intensity I^*_{out}; (ii) I^*_{out} is not affected by the presence of other light absorbers and can be measured in monoculture; (iii) the species with the lowest I^*_{out} will competitively exclude all other species; (iv) I^*_{out} is negatively related to the light supply; and (v) the outcome of competition may depend on the light supply.

The present paper intended to investigate the robustness of these predictions. For this purpose, we developed a model formulated in more general terms. In essence, we only assumed:

- a biomass distribution that is continuous over depth but otherwise quite arbitrary (Assumption 1);
- a light gradient that is one-dimensional and uni-directional (Assumption 2);
- a carbon gain rate that is positively related to the local light intensity (Assumption 3);
- a growth dynamics that is determined by the carbon balance (Assumption 4).

We have shown that these qualitative assumptions are sufficient to derive all the predictions mentioned above. However, we had to postulate that all species have a similar distribution over the light gradient. Spatial differentiation of the competitors may lead to a completely different situation: the critical light intensities of the competitors are no longer sufficient to predict the outcome of competition, and equilibrium co-existence of several species on a single resource may occur.

Summarizing, we conclude that the results of our previous paper are quite robust. They do not depend on specific assumptions such as Lambert-Beer's law or the Monod equation, but reflect far more general principles of light-limited growth. However, competitive exclusion crucially depends on the parallel distribution of the competitors as externally imposed by mixing.

LIMITATIONS OF THE MODEL ASSUMPTIONS

It is obvious that several important aspects of light-limited growth and competition have not been addressed. For example, our model neglects the daily and seasonal fluctuations in the light supply, the spectral distribution of light, time delays in the adaptation to local light availability, seedling establishment under a dense canopy, and the spatial stochasticity of light gaps in forest vegetations. Here we discuss some aspects that are more closely related to our model assumptions.

The assumption that the light flux is uni-directional (Assumption 2.2) makes the nature of the light gradient more transparent. This assumption made it possible to introduce the concept of "quantum return" and to formulate light-limited growth directly in terms of the light gradient. A direct interpretation in terms of light availability contributes to a better intuitive understanding of light limitation, and our main results (Results 4, 5, and 8) follow easily from this formulation. However, although Assumption 2.2 simplifies the analysis, it can be shown that Assumption 2.1 is sufficient to derive all our results. The only exception is Result 4: if the light flux is not uni-directional, the relation between I^*_{out} and I_{in} need not be negative (but see Appendix B).

We have focused on a light gradient in one dimension. However, processes such as scattering and reflection may lead to a multi-dimensional light field. As long as the vertical component of the light flux is prevalent, the conclusions of our model will hardly be affected (cf. Iehana, 1983; Gordon, 1989). If other dimensions cannot be neglected, the formalism becomes more involved (e.g. Kirk, 1983; Evers, 1991). In this case, it is not obvious whether a single parameter, analogous to I^*_{out}, is able to summarize the light requirements of a species. Even in a multi-dimensional light field, however, we conjecture that competitive exclusion still holds in the absence of spatial differentiation.

We have assumed that the specific carbon gain rate is positively related to the local light intensity. When our formalism is applied to a non-motonic light-response curve (e.g. photo-inhibition), the global stability of the equilibria is no longer guaranteed. Instead, several stable equilibria may exist, and the outcome of competition may depend on the initial conditions (see Butler & Wolkowicz, 1985, for a similar situation in the context of nutrient inhibition).

The assumption that the specific carbon gain rate depends *only* on the local light intensity is not always justified. In uni-cellular algae, the specific carbon gain may not only depend on light availability but also on cell biomass, for example, if carbon uptake is determined by the cell surface area whereas carbon losses are determined by the cell volume (cf. Metz *et al.*, 1988). In the context of higher plants, the carbon allocation strategy may be influenced by global aspects such as total biomass or the light supply. If g is affected by the light supply, our results still hold. The only exception is, again, Result 4: if g is a function of I *and* I_{in}, the relation between I^*_{out} and I_{in} need not be negative. In contrast, it is not obvious which of our results remain to hold if g also depends on biomass.

SPATIAL HETEROGENEITY AND SPATIAL DIFFERENTIATION

Many studies conclude that equilibrium co-existence on a single, homogeneously distributed resource is not possible (e.g. Armstrong & McGehee, 1980; Tilman, 1982). In contrast, several species may co-exist on a single resource in a spatially heterogeneous environment (e.g. Jäger *et al.*, 1987; Ives, 1988; Tilman, 1994). The spatial heterogeneity of a light gradient may be a major factor contributing to the species diversity observed in aquatic and terrestrial plant communities (e.g. Hudon & Bourget, 1983; Terborgh, 1985; Kohyama, 1993). We have shown, however, that the spatial heterogeneity in resource availability *per se* is not sufficient to explain co-existence. Our model still predicts competitive exclusion if the species have a similar distribution over the light gradient. This demonstrates that the spatial heterogeneity in light availability must be combined with spatial differentiation of the competitors in order to explain species co-existence.

In the absence of spatial differentiation, the light requirements of the competitors are decisive for the outcome of competition. It seems unlikely, however, that a parallel distribution can be maintained if it is not externally imposed by mixing. In fact, processes such as differential growth or diffusion may easily lead to spatial differentiation. These processes have not been explicitly addressed in this paper. Instead, we have considered the relative positions of the competitors as given. The next logical step would be to study how spatial patterns are generated. As soon as spatial patterns emerge, a slightly better position in the light gradient may provide an enormous competitive advantage. Accordingly, the allocation and migration strategies of the competitors may become as important for the outcome of competition as their minimal light requirements.

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APPENDIX A

Properties of a Uni-directional Light Flux

In this appendix, we show that, in case of a uni-directional light flux, the light absorption per unit biomass, $\mathrm{d}I/\mathrm{d}w$, only depends on the local light intensity $I = \varphi(I_{\mathrm{in}}, kw)$. In other words, it does not depend on the light supply I_{in} and the cumulative biomass w by which the local light intensity is induced.

LEMMA

If light absorption is governed by $I = \varphi(I_{\mathrm{in}}, kw)$, where φ satisfies Assumption 2, light absorption per unit biomass can be written as

$$\frac{\mathrm{d}I}{\mathrm{d}w} = -ka(I),$$

where a is a positive function of the light intensity I.

Proof

In order to make the proof as transparent as possible, we denote the first argument of φ by x (i.e. $x = I_{\mathrm{in}}$) and the second by y (i.e. $y = kw$). Light absorption per unit biomass can then be written as

$$\frac{\mathrm{d}I}{\mathrm{d}w} = \frac{\mathrm{d}\varphi}{\mathrm{d}w}(I_{\mathrm{in}}, kw) = \frac{\partial\varphi}{\partial y}(x, y)\frac{\mathrm{d}y}{\mathrm{d}w} = k\frac{\partial\varphi}{\partial y}(x, y).$$

If we can show that $\partial\varphi/\partial y$ only depends on I, our lemma is proved since the function a may then be defined by

$$a(I) = -\frac{\partial\varphi}{\partial y}(x, y). \qquad \text{(A.1)}$$

$a(I)$ is positive in view of $\partial\varphi/\partial y < 0$ (Assumption 2.1).

We now show that $\partial\varphi/\partial y$ only depends on I and not on the combination of x and y by which $I = \varphi(x, y)$ is induced. Consider two different combinations (x, y) inducing the same light intensity:

$$I = \varphi(x_1, y_1) = \varphi(x_2, y_2). \qquad \text{(A.2)}$$

The required relation

$$\frac{\partial\varphi}{\partial y}(x_1, y_1) = \frac{\partial\varphi}{\partial y}(x_2, y_2) \qquad \text{(A.3)}$$

is a direct consequence of Assumption 2.2: in view of (11), the identity

$$\varphi(\varphi(x_1, y_1), \Delta y) = \varphi(\varphi(x_2, y_2), \Delta y)$$

leads to

$$\varphi(x_1, y_1 + \Delta y) = \varphi(x_2, y_2 + \Delta y).$$

Together with (A.2), this implies

$$\frac{\varphi(x_1, y_1 + \Delta y) - \varphi(x_1, y_1)}{\Delta y} = \frac{\varphi(x_2, y_2 + \Delta y) - \varphi(x_2, y_2)}{\Delta y}.$$

Equation (A.3) is obtained by taking limits on both sides $(\Delta y \to 0)$. □

Note that Assumption 2.2 resembles the group property of an autonomous dynamical system with kw as time and I_{in} as initial condition. Hence the lemma restates that such a dynamical system is generated by an autonomous differential equation (see, for example, Hirsch & Smale, 1974).

APPENDIX B

Alternative Formulations of the Light Gradient

Under certain special conditions, our formalism can be extended to light absorption functions that do not describe a uni-directional light flux in the sense of Assumption 2.2. As an example, consider the light absorption function proposed by Reynolds & Pacala (1993):

$$I(w) = \varphi(I_{\text{in}}, kw) = \frac{I_{\text{in}}}{1 + kw}. \tag{B.1}$$

It is easily verified that this function does not satisfy Assumption 2.2. Accordingly, light absorption per unit biomass, $\mathrm{d}I/\mathrm{d}w$, does not only depend on the local light intensity but also on the light supply:

$$\frac{\mathrm{d}I}{\mathrm{d}w} = -k\frac{I_{\text{in}}}{(1 + kw)^2} = -k\frac{I^2}{I_{\text{in}}}. \tag{B.2}$$

Notice, however, that eqn (B.2) is of the form

$$\frac{\mathrm{d}I}{\mathrm{d}w} = -ka(I)b(I_{\text{in}}), \tag{B.3}$$

where a and b are both positive functions. In other words, the dependence on the light supply I_{in} can be separated from the dependence on the local light intensity I. As a consequence, the total carbon gain rate can still be written as an integral over the light gradient:

$$G(I_{\text{out}}) = \frac{1}{b(I_{\text{in}})}\int_{I_{\text{out}}}^{I_{\text{in}}} \frac{g(I)}{ka(I)}\,\mathrm{d}I. \tag{B.4}$$

It is easy to see that all our conclusions, including Results 4 and 5, can also be derived from eqn (B.4). In other words, even if a light absorption function does not describe a uni-directional light flux, it is still captured by our formalism if it satisfies eqn (B.3).

APPENDIX C

Competitive Exclusion

We shall now prove that, in the absence of spatial differentiation, the species with the lowest critical light intensity I^*_{out} competitively excludes all other species (Result 8). A similar proof for competitive exclusion is given by Armstrong & McGehee (1980: appendix D) in the context of nutrient competition.

Consider n species that are distributed in parallel. We assume that species 1 has the lowest critical light intensity:

$$I^*_{\text{out},1} < I^*_{\text{out},i} \quad \text{for } i = 2, \ldots, n,$$

and that species 1 is able to grow in monoculture: $I_{\text{in}} > I_{\text{C},1}$. Our goal is to show that, independent of the initial value of I_{out}, the system will always converge to the monoculture equilibrium of species 1, at which $I_{\text{out}} = I^*_{\text{out},1}$.

In view of Result 6, species 1 will increase if I_{out} is above its critical light intensity. In other words, $I_{\text{out}} > I^*_{\text{out},1}$ implies

$$\frac{\mathrm{d}W_1}{\mathrm{d}t} > 0. \tag{C.1}$$

If, on the other hand, I_{out} is below the critical light intensity of species 1, all species will decrease and I_{out} will increase. More precisely, $I_{\text{out}} \leqslant I^*_{\text{out},1}$ implies

$$\frac{\mathrm{d}I_{\text{out}}}{\mathrm{d}t} = \sum_j \frac{\partial I_{\text{out}}}{\partial W_j}\frac{\mathrm{d}W_j}{\mathrm{d}t} \geqslant 0, \tag{C.2}$$

with equality only at the monoculture equilibrium of species 1.

Suppose for the moment that I_{out} remains below $I^*_{\text{out},1}$ for all time. In this case, I_{out} remains to increase [see (C.2)] and thus converges to its upper bound $I^*_{\text{out},1}$. Hence, I_{out} may be viewed as a Lyapunov function, and the system approaches the monoculture equilibrium of species 1. We now suppose that I_{out} becomes larger than $I^*_{\text{out},1}$. Equation (C.2) shows that, once I_{out} is larger than $I^*_{\text{out},1}$, it will remain larger than $I^*_{\text{out},1}$ for all time. Hence the set given by $I_{\text{out}} > I^*_{\text{out},1}$ is positively invariant. W_1 is a Lyapunov function on this set; in view of (C.1), W_1 will remain to increase and converge to its upper bound, the monoculture equilibrium of species 1.

Hence, independent of the initial value of I_{out}, species 1 will always converge to its monoculture equilibrium, at which $I_{\text{out}} = I^*_{\text{out},1}$ and all other species are extinct.