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The models of Berendse and Tilman: two different perspectives on plant competition?

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Introduction

Plant competition for limiting nutrients has been approached from a wide variety of perspectives (e.g. Baldwin 1976; Nye & Tinker 1977; Chapin 1980; Berendse 1985; Tilman 1988; Grime 1991). This is nicely illustrated in the book *Perspectives on Plant Competition* (Grace & Tilman 1990), where two adjacent chapters deal with two independently developed models of plant competition.

Berendse & Elberse (1990) relate plant growth to the nutrient supply. Their model, first presented by Berendse (1985), is an extension of the classical competition theory of De Wit (1960). In addition to the nutrient supply, Berendse & Elberse emphasize the impact of nutrient losses from the plants on the outcome of competition (cf. Berendse & Aerts 1987). These losses may be due to abscission of leaves, turnover of roots, herbivory, etc. They consider the 'relative nutrient requirement', defined as the amount of nutrients needed to maintain or replace each unit of biomass during a given time period, as a major determinant of competitive success.

Tilman (1990) relates plant growth to the nutrient concentration in soil solution. His approach is an extension of studies on nutrient competition among micro-organisms in the chemostat (e.g. Hsu, Hubbell & Waltman 1977; Tilman 1977). Tilman emphasizes nutrient reduction as the mechanism of nutrient competition. He presents five models which all lead to the prediction that the 'critical nutrient concentration' R^* is the key parameter of competitive success. R^* can be measured as the concentration in the soil to which a limiting nutrient is reduced by a steady-state monoculture.

These two models seem to represent two completely different perspectives on plant competition. The authors not only use a different terminology and notation, they also emphasize different plant characteristics and soil properties. Potentially, such divergent approaches might provide further fuel for the current controversies about the nature of plant competition (e.g. Thompson 1987; Tilman 1987, 1988; Grime 1988; Campbell *et al.* 1991). Yet both models deal with the same phenomenon: plants competing for

a single limiting nutrient. Hence van Andel (1992, p. 176) asserted that these two models 'must have much in common. Perhaps the different terminology and notation, related to the origins of the models, exaggerates the actual differences (cf. Grace 1991).

In this paper, I argue that these two models have indeed much in common. More precisely, I demonstrate that Berendse's model can be interpreted as a special case of Tilman's model. For this purpose, I first present the models in a similar notation and try to eliminate differences in terminology. A survey of my notation is given in Table 1.

Tilman's model

The structure of Tilman's (1977, 1990) model reads as follows:

biomass dynamics:

$$dW/dt = \text{growth} - \text{losses} \quad \text{eqn 1}$$

nutrient dynamics:

$$dR/dt = \text{supply} - \text{consumption} \quad \text{eqn 2}$$

BIOMASS DYNAMICS

In Tilman's model, the biomass dynamics of each species i is written in the general form:

$$\frac{dW_i}{dt} = W_i [f_i(R) - m_i] \quad \text{eqn 3}$$

where W_i is the biomass of species i , $f_i(R)$ is the specific growth rate as a function f_i of the nutrient concentration R in soil solution, and m_i is the specific biomass loss rate. Notice that this formulation explicitly states that all species face the same soil nutrient concentration. Thus, it is assumed that any spatial heterogeneity of the soil solute can be neglected.

NUTRIENT DYNAMICS

The dynamics of the nutrient concentration in soil solution is given by:

$$\frac{dR}{dt} = Y(R) - \sum_{j=1}^n Q_j W_j f_j(R) \quad \text{eqn 4}$$

where $Y(R)$ is the nutrient supply rate as a function of the soil nutrient concentration, Q_j is the tissue nutrient

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Table 1. Notation and terminology

Symbol	Interpretation
a_i	rate constant
f_i	specific growth rate
k_i	partitioning coefficient
L_i	specific nutrient loss rate
m_i	specific biomass loss rate
Q_i	tissue nutrient concentration of plant biomass
R	nutrient concentration in soil solution
W_i	plant biomass
Y	nutrient supply rate

concentration of species j and n is the total number of species.

FURTHER SPECIFICATIONS

Typically, Tilman assumes that the specific growth rate, $f_i(R)$, has the form of a Michaelis–Menten function:

$$f_i(R) = f_{\max, i} \frac{R}{h_i + R} \quad \text{eqn 5}$$

where $f_{\max, i}$ is the maximum specific growth rate, and h_i is the soil nutrient concentration required for growth at half the maximum rate. The precise shape of the functions $f_i(R)$, however, is not important for Tilman's predictions. The Michaelis–Menten function is not required. It is sufficient that the specific growth rate is a monotonically increasing function of the nutrient concentration (Armstrong & McGehee 1980; Butler & Wolkowicz 1985). Thus, the functions $f_i(R)$ may be rather complex; they may incorporate a plant's morphology, physiology, allocation, etc. (Tilman 1990).

In Tilman's models, the supply rate is usually of the chemostat type:

$$Y(R) = D(S - R) \quad \text{eqn 6}$$

where S is a parameter and D is a rate constant. In the chemostat, S is the nutrient concentration of the inflow, R is the nutrient concentration within the culture vessel and D is the dilution rate. For Tilman's predictions we are not committed to this chemostat equation. It is sufficient that the dynamics lead towards a globally stable equilibrium, which is the case for a wide class of abiotic resource models (Armstrong & McGehee 1980).

PREDICTIONS

The biomass dynamics (equation 3) of each species i can be characterized by the relation between the actual soil nutrient concentration R and a 'critical nutrient concentration' R_i^* , which is defined by $f_i(R_i^*) = m_i$ (see Fig. 1). The biomass of species i will increase if $R > R_i^*$, will decrease if $R < R_i^*$ and remains

stationary if $R = R_i^*$. Accordingly, R_i^* is a parameter which translates a species' physiological, morphological and life-history traits into a minimum subsistence level for plant growth. However, R_i^* is not only a theoretical construct. It can be measured as the concentration to which the limiting nutrient is reduced by a steady-state monoculture of the species concerned (Tilman 1990; Tilman & Wedin 1991a).

Tilman's model predicts that the species with lowest R_i^* will competitively exclude all other species. Rigorous formal proofs can be found in the theoretical literature (e.g. Hsu *et al.* 1977; Armstrong & McGehee 1980; Butler & Wolkowicz 1985), but the basic idea is simple. Let the species be labelled such that species 1 has the lowest R_i^* , i.e. $R_1^* < R_2^* < \dots < R_n^*$. As long as $R > R_i^*$, species 1 will increase. With increasing plant biomass, the nutrient concentration in soil solution will be reduced. Hence, in the long run, species 1 will be able to deplete the soil nutrient concentration below the critical nutrient concentrations of the other species. As a consequence, all species, except species 1, will decrease. This will continue until all species, except species 1, have disappeared while species 1 approaches a steady state at which $R = R_1^*$.

EXPERIMENTAL SUPPORT

This general prediction is supported by much experimental evidence, mainly from laboratory studies with bacteria (Hansen & Hubbell 1980), phytoplankton (Tilman 1977; Tilman, Mattson & Langer 1981) and zooplankton (Rothhaupt 1988). Recently, Tilman & Wedin (1991a,b; Wedin & Tilman 1993) performed field experiments with five perennial grass species which also support this prediction. The grasses were grown in monoculture and pairwise mixtures under nitrogen-limited conditions in a sandy soil. The R_i^* were measured as the concentration to which the monocultures of each species reduced soil nitrate and ammonium. In all mixtures, the grass species with

Fig. 1. Specific growth rate, $f_i(R)$, and specific loss rate, m_i , as a function of the nutrient concentration in soil solution. The specific growth and loss rate balance at the critical nutrient concentration R_i^* .

lowest R_i^* , as measured in monoculture, displaced the other species. The displacement was slowest for the species pair with the most similar R_i^* values.

Berendse's model

In contrast to Tilman (1990), Berendse & Elberse (1990) only consider the biomass dynamics:

$$dW/dt = \text{growth} - \text{losses} \quad \text{eqn 7}$$

while the nutrient concentration in soil solution is not explicitly taken into account.

BIOMASS DYNAMICS

Berendse emphasizes the nutrient balance of the plant species. He assumes that plant densities are sufficiently high to absorb all nutrients which become available by the mineralization process. Accordingly, the nutrient supply rate Y must be partitioned between the species. Following De Wit (1960), the nutrient uptake rate of each species i is therefore given by:

$$\frac{k_i W_i}{\sum_{j=1}^n k_j W_j} Y \quad \text{eqn 8}$$

where the coefficients k_i describe the partitioning of the nutrient supply among the n competing species (Berendse 1993). For example, if plant species would be identical except for, say, root diameter, the partitioning coefficients k_i would represent the specific root lengths of the species. In the context of two competing species, the partitioning coefficients k_1 and k_2 are usually replaced by a 'relative competition coefficient' k_{12} defined as the ratio k_1/k_2 (Berendse & Elberse 1990).

The nutrient losses of each species i are given by $L_i W_i$, i.e. the product of biomass W_i and the so-called 'relative nutrient requirement' L_i . Perhaps the term 'requirement' is not so appropriate. Formally, L_i represents a nutrient loss rate per unit biomass. Therefore, I prefer to use a more neutral term like 'specific nutrient loss rate'.

If plant biomass is proportional to the total amount of nutrients in the plant, the biomass dynamics can be written as:

$$\frac{dW_i}{dt} = \frac{1}{Q_i} \left(\frac{k_i W_i}{\sum_{j=1}^n k_j W_j} Y - L_i W_i \right) \quad \text{eqn 9}$$

where Q_i is the tissue nutrient concentration (Berendse 1993).

PREDICTIONS

Berendse & Elberse (1990) predict that, in case of

only two species, species 1 will competitively exclude species 2 if:

$$k_1/k_2 > L_1/L_2 \quad \text{eqn 10}$$

whereas species 2 will displace species 1 if this inequality is reversed. In other words, the species with lowest L_i/k_i will win the competition.

In general, the principles governing the competition between two species need not hold if there are more than two competitors (e.g. May & Leonard 1975; Arneodo *et al.* 1982). In case of Berendse's model, however, the above prediction can be generalized to any number of species: if n species compete for the same nutrient supply, the species with lowest L_i/k_i will displace all other species. (A formal proof is given in the Appendix.)

EXPERIMENTAL SUPPORT

During the last decades, vegetations dominated by *Erica tetralix* L. have been replaced by monocultures of the grass *Molinia caerulea* (L.) Moench in many wet heathlands in the Netherlands. In order to study the effects of an increased atmospheric nitrogen deposition on the competition between *Molinia* (m) and *Erica* (e), Berendse & Aerts (1984) carried out some competition experiments. They found that the relative competition coefficient ranged from $k_{me} = 1.2$ under unfertilized conditions to $k_{me} = 5$ at a high nitrogen supply. Berendse, Oudhof & Bol (1987) measured that the 'relative nitrogen requirement' of *Molinia* is about three times as high as that of *Erica*, i.e. $L_m/L_e = 3$. Hence, in view of equation 10, *Erica* should win the competition under unfertilized conditions (as $k_{me} < L_m/L_e$), whereas *Molinia* should win at a high nitrogen supply (at which $k_{me} > L_m/L_e$). This closely fits the field situation. Most heathlands have also been grazed by sheep until the first part of this century. As sheep prefer *Molinia*, sheep grazing will mainly increase the nitrogen losses of *Molinia* (i.e. the ratio L_m/L_e becomes larger) which shifts the competitive dominance in favour of *Erica* (Berendse 1985). Thus, the rapid replacement of *Erica*-dominated communities by monocultures of *Molinia* is probably related to both the increased atmospheric nitrogen deposition and the cessation of sheep grazing.

The two models compared

A SPECIFIC VERSION OF TILMAN'S MODEL ...

I shall now show that the model of Berendse is a special case of Tilman's model. It is a special case in the sense that the following three specifications of Tilman's general model lead to Berendse's formulation:

1. Fast dynamics of nutrients in soil solution. Berendse does not take the dynamics of the soil solute into account, but instead assumes that plant densities are sufficiently high to absorb the total nutrient supply. In the context of Tilman's model, this implies that the dynamics of the soil solute is much faster than the dynamics of the growing plants. In other words, the nutrient concentration in soil solution adjusts very quickly to that level at which the nutrient supply is balanced by the nutrient uptake of the plants. More precisely, this 'quasi-steady-state' approximation can be written as (e.g. Segel 1984):

$$\frac{dR}{dt} \approx 0 \quad \text{eqn 11}$$

This approximation does not imply that the nutrient concentration remains constant all time. It only states that the soil solute is essentially in equilibrium with nutrient supply and nutrient uptake. If, for example, the total nutrient uptake increases, the nutrient concentration in soil solution rapidly drops until a new quasi-steady-state level is reached.

2. Linear response. The specific growth rate increases linearly with the nutrient concentration in soil solution, i.e.:

$$f_i(R) = a_i R \quad \text{eqn 12}$$

where a_i is a rate constant. This assumption may seem rather unrealistic. A nonlinear Michaelis-Menten term, for example, may look more attractive. If the nutrient concentration in the rooting zone is very low, however, the nutrient uptake rate is usually not limited by the maximum nutrient uptake capacities of the root (Chapin 1980). More precisely, for $R \ll h_i$ the Michaelis-Menten equation 5 reduces to equation 12, with $a_i = f_{\max,i}/h_i$. Accordingly, several models of the soil-root system have adopted this linear approximation (e.g. Nye & Tinker 1977).

3. Constant nutrient supply. The nutrient supply rate is independent of the nutrient concentration in soil solution, i.e.:

$$Y(R) = Y \quad \text{eqn 13}$$

This seems a minor restriction. It is only introduced to show the relationship between the models of Tilman and Berendse.

... LEADS TO BERENDSE'S MODEL

Given the three specifications mentioned above, Berendse's model can be derived from Tilman's model. In view of the nutrient dynamics (equation 4), $dR/dt \approx 0$, $f_i(R) = a_i R$ and $Y(R) = Y$, the quasi-steady-state nutrient concentration can be obtained by solving:

$$\frac{dR}{dt} = Y - \sum_{j=1}^n Q_j W_j a_j R = 0 \quad \text{eqn 14}$$

This yields:

$$R = \frac{Y}{\sum a_j Q_j W_j} \quad \text{eqn 15}$$

Thus, R increases with the nutrient supply but decreases with increasing biomass.

In view of $f_i(R) = a_i R$, the biomass dynamics (equation 3) of Tilman's model reads:

$$\frac{dW_i}{dt} = W_i (a_i R - m_i) \quad \text{eqn 16}$$

Substituting equation 15 into equation 16 yields:

$$\frac{dW_i}{dt} = \frac{a_i W_i}{\sum a_j Q_j W_j} Y - m_i W_i \quad \text{eqn 17}$$

This specific version of Tilman's model now resembles Berendse's model (equation 9). A biomass loss rate of m_i units in Tilman's notation corresponds with a biomass loss rate of L_i/Q_i units in Berendse's notation. Hence $m_i = L_i/Q_i$. Furthermore, in Tilman's model we have a parameter a_i , while Berendse defines a parameter k_i . This is just a matter of notation. If we use the same parameter notation for both models, for example by the parameter transformations $a_i = k_i/Q_i$ and $m_i = L_i/Q_i$, equation 17 can be rewritten as:

$$\frac{dW_i}{dt} = \frac{1}{Q_i} \left(\frac{k_i W_i}{\sum k_j W_j} Y - L_i W_i \right)$$

which is just Berendse's model (equation 9). Hence, I have shown that the model of Berendse is a special case of Tilman's general model.

Consequently, Berendse's model and the corresponding simplified version of Tilman's model must lead to similar predictions. This can be verified as follows: Tilman's model predicts that the species with lowest R_i^* wins the competition. Given equation 16, $R_i^* = m_i/a_i$. In view of $m_i = L_i/Q_i$ and $a_i = k_i/Q_i$, the species with lowest R_i^* in Tilman's model corresponds to the species with lowest L_i/k_i in Berendse's model. As shown in the Appendix, the species with lowest L_i/k_i is indeed the superior competitor in Berendse's model.

VALIDATION OF THE QUASI-STEADY-STATE APPROXIMATION

The crucial step made above is a reduction of the nutrient dynamics (equation 4) to the algebraic equation 15. I shall now investigate for what range of parameter values this quasi-steady-state approximation can be justified. For simplicity, the analysis is restricted to a single species. In view of equations 12 and 13, Tilman's model is then given by:

$$\frac{dR}{dt} = Y - a Q W R \quad \text{eqn 18a}$$

$$\frac{dW}{dt} = W (a R - m) \quad \text{eqn 18b}$$

Following Segel (1984), let us a priori assume that the nutrient dynamics is much faster than the biomass dynamics. Afterwards, we can see when this assumption is valid.

If the nutrient dynamics is much faster than the biomass dynamics, biomass will hardly change on a short time scale, i.e. $W(t) \approx \hat{W} = \text{constant}$. The nutrient dynamics (equation 18a) is then given by:

$$\frac{dR}{dt} = Y - aQ\hat{W}R$$

which can be solved as:

$$R(t) = \frac{Y}{aQ\hat{W}} - \left(\frac{Y}{aQ\hat{W}} - R_0 \right) e^{-aQ\hat{W}t} \quad \text{eqn 19}$$

Thus, from the exponential in equation 19, the time-scale associated with the nutrient dynamics is $1/aQ\hat{W}$.

On a long time-scale, the nutrient concentration is essentially in equilibrium, i.e. $dR/dt = 0$. This yields

$$R = \frac{Y}{aQ\hat{W}}$$

The biomass dynamics (equation 18b) is therefore given by:

$$\frac{dW}{dt} = \frac{Y}{Q} - mW$$

which can be solved as:

$$W(t) = \frac{Y}{Qm} - \left(\frac{Y}{Qm} - W_0 \right) e^{-mt} \quad \text{eqn 20}$$

Hence the time-scale associated with the biomass dynamics is $1/m$.

Thus, the dynamics of the nutrient concentration in soil solution is much faster than the dynamics of the growing plants if:

$$m \ll aQ\hat{W} \quad \text{eqn 21}$$

where m is the specific biomass loss rate and $aQ\hat{W}$ is a measure of the total nutrient uptake of the vegetation. Notice that the condition in equation 21 can only be satisfied if plant biomass $\hat{W}$ is sufficiently high, in line with Berendse's assumptions. Interestingly, the species with lowest $R^* = m/a$ is favoured by competition. Hence, nutrient competition promotes the condition (equation 21) required for a quasi-steady-state approximation.

Discussion

The competition model of Berendse (1985, 1993) is based on the assumption that plant growth can be related directly to the nutrient supply. The dynamics of the soil solute is not explicitly taken into account. Instead, the nutrient supply is simply partitioned among the competing species. At first sight, this approach seems incompatible with Tilman's (1990) model, where plants compete through their effect on the nutrient concentration in soil solution. I have

shown, however, that Tilman's model leads to the resource partitioning of Berendse's model if the following simplifying assumptions are made: (1) the dynamics of the nutrient concentration in soil solution is much faster than the dynamics of the growing plants, (2) the nutrient uptake rate is a linear function of the nutrient concentration in soil solution and (3) the nutrient supply rate is independent of the nutrient concentration in soil solution. This seems a fairly reasonable approximation if plant densities are sufficiently high to absorb the total nutrient supply and if the nutrient concentration in the rooting zone is sufficiently low to ensure that saturation of the nutrient uptake rate can be neglected. For practical purposes, however, further research will be required to assess in which plant communities these conditions are really met. In particular, it is not yet clear to what extent saturation of the nutrient uptake rate can indeed be neglected in nutrient-poor environments.

The demonstration that Berendse's model can be interpreted as a special case of Tilman's model implies that these two models are fully compatible (though not identical as Tilman's model can be written in a far more general form). In principle, however, resource partitioning could be brought about by other mechanisms as well. The conclusion that Berendse's model can be derived from Tilman's model does not necessarily imply that it is impossible to derive Berendse's model from other considerations.

There is an interesting contrast between the experimental approaches of Tilman and Berendse. Tilman predicts the outcome of competition from characteristics measured in monoculture. He emphasizes that it is not necessary to perform competition experiments to estimate 'competition coefficients' or other interaction terms if species only interact via shared resources (Tilman 1990). According to Tilman, all relevant parameters concerned with resource utilization should be measurable in monoculture. In contrast, Berendse uses competition experiments to estimate the relative competition coefficient $k_{12} = k_1/k_2$, although the specific nutrient loss rates are measured in monoculture stands. In principle, if plant species differ in one or only a few respects, the k_i 's represent simple physiological or morphological plant features that should be measurable in monoculture (Berendse & Elberse 1990). In the present paper, for example, k_{12} corresponds to the ratio a_1Q_1/a_2Q_2 , i.e. the ratio of the 'nutrient affinities' of the two species. Berendse argues, however, that plant species may differ in so many respects that, usually, the relative competition coefficient may better be estimated in competition experiments. In my opinion, both arguments make sense. On the one hand, care should be taken that the underlying competition model matches the mechanisms by which the species interact. For this reason, direct measurements of all relevant plant characteristics and soil properties should be preferred. On the

other hand, it is not yet clear how far we can get with such a mechanistic approach.

By emphasizing some features of reality while ignoring many others, simple models can only provide a first step towards the understanding of complex systems like natural plant communities. Let me indicate a few aspects which may be relevant for a further understanding of nutrient competition. First, Tilman's model is based on the assumption that spatial heterogeneity of the soil solute is negligible. This may be a suitable approximation for mobile ions like nitrate, in line with the experiments of Tilman & Wedin (1991a,b; Wedin & Tilman 1993) where nitrogen was the only limiting factor. In case of far less mobile ions like phosphate, however, many local depletion zones will develop in the rooting zone (e.g. Nye & Tinker 1977; Barber 1984). Perhaps the predictions of Tilman and Berendse still apply if an appropriate 'averaging' over all these local depletion zones can be justified, but a rigorous competition theory concerned with such soil heterogeneities is not yet available. Second, some plant species may profit from nutrients unavailable for other species, by modification of the nutrient availability in their rhizosphere or via mycorrhizal associations (e.g. Allen & Allen 1990). Similarly, plants which root deeply can absorb nutrients not available for plants with a shallower root system (Berendse 1982). In principle, such mechanisms may promote coexistence if the 'inferior' competitors have access to 'refugia' where they exploit resources unavailable for the other species. Third, the competition dynamics can be altered considerably as soon as competition for light also becomes involved (Olff, Huisman & van Tooren 1993; Wedin & Tilman 1993; Huisman & Weissing 1994). This may be relevant even under rather nutrient-poor conditions as plants may already shade each other when biomass is quite low. These aspects deserve further attention in the next generation of plant competition models.

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Appendix. Prediction of Berendse's model

In the model of Berendse (1985, 1993), the competition between n species is characterized by the following dynamical system:

$$\frac{dW_i}{dt} = \frac{1}{Q_i} \left(\frac{k_i W_i}{\sum_{j=1}^n k_j W_j} Y - L_i W_i \right) \quad \text{eqn 9}$$

In this Appendix, I give a formal proof that the species with lowest L_i/k_i competitively displaces all other species.

Equation 9 is of the general form:

$$\frac{1}{W_i} \frac{dW_i}{dt} = \varepsilon_i G(W_1, \dots, W_n) - \gamma_i \quad \text{eqn A1}$$

with $\varepsilon_i = k_i/Q_i$, $\gamma_i = L_i/Q_i$ and $G(W_1, \dots, W_n) = \frac{Y}{\sum k_j W_j}$.

It is obvious that equation 9 is not identical with the 'Lotka-Volterra' competition models found in most textbooks. But equation A1 differs only slightly from Volterra's (1928) original model and the following proof closely resembles Volterra's derivation of the competitive exclusion principle.

Equation A1 can be rewritten as:

$$\frac{Q_i}{k_i} \frac{1}{W_i} \frac{dW_i}{dt} = G(W_1, \dots, W_n) - \frac{L_i}{k_i}$$

which implies:

$$\frac{d \ln W_i^{\frac{Q_i}{k_i}}}{dt} = G(W_1, \dots, W_n) - \frac{L_i}{k_i} \quad \text{eqn A2}$$

The dynamics of two arbitrary species a and b of our competitive system of n species can be followed by looking at, from equation A2:

$$\frac{d \ln W_a^{\frac{Q_a}{k_a}}}{dt} - \frac{d \ln W_b^{\frac{Q_b}{k_b}}}{dt} = \frac{L_b}{k_b} - \frac{L_a}{k_a}$$

which can be solved as:

$$\frac{W_a^{\frac{Q_a}{k_a}}}{W_b^{\frac{Q_b}{k_b}}} = C e^{(\frac{L_b}{k_b} - \frac{L_a}{k_a})t} \quad \text{eqn A3}$$

where C is a positive constant.

Let the species be labelled such that species 1 has the lowest value of L/k , i.e.:

$$\frac{L_1}{k_1} < \frac{L_2}{k_2} < \dots < \frac{L_n}{k_n}$$

If we now apply equation A3 to species 1 and another arbitrary species of our competitive system, say species b (where $b \neq 1$), we will have:

$$\lim_{t \rightarrow \infty} \frac{W_1^{\frac{Q_1}{k_1}}}{W_b^{\frac{Q_b}{k_b}}} = \infty \quad \text{eqn A4}$$

Hence, independent of the initial conditions, either the biomass of species 1 will grow to infinity or the biomass of species b approaches zero. In view of equation 9, however, the nutrient uptake is limited by the nutrient supply rate Y whereas the nutrient losses may increase without bound. As a consequence, the biomass of species 1 cannot grow to infinity, and, thus, species b must be driven to zero.

But this argument holds true for every arbitrary species b (where $b \neq 1$). In other words, all species will disappear except species 1. This demonstrates that the species with lowest L_i/k_i competitively excludes all other species.