Integrating the production functions of Liebig, Michaelis–Menten, Mitscherlich and Liebscher into one system dynamics model

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Abstract

Any agricultural production process is characterized by input–output relations. In this paper we show that the production functions of Liebig, Mitscherlich and Liebscher for the relation between nutrient supply and crop production can be regarded as special variants of one 'integrated model'. The model is elaborated for two nutrients, nitrogen and phosphorus, and is based on the Michaelis–Menten hyperbolic equation. This basic equation has two main terms and one multiplicative interaction term. The parameter values determine which one of the aforementioned functions is generated. 'Greenwood's variant of the Michaelis–Menten function' is approached if the main terms dominate. 'De Wit's variant of the Mitscherlich function' is approached if the multiplicative term dominates. Liebig's function emerges from any of these variants if nutrient supply is constrained to such an extent that nutrient uptake continually exhausts the nutrient stock. The 'Liebscher variant' – considered the most appropriate for most empirical situations – is intermediate between those of Liebig, Michaelis–Menten and 'De Wit's Mitscherlich', and can be obtained by parameter calibration. Generally, these functions result in 'decreasing marginal returns' with increasing nutrient supply. However, if interacting nutrients are supplied in precisely the required proportion, the variant with a multiplicative term does show 'increasing marginal returns', but only in conditions of low nutrient supply rates, low nutrient affinities and / or high nutrient losses.

Additional keywords: crop production, nutrient losses, nutrient productivity, nutrient uptake, proportional supply of nutrients, resource use efficiency, responsive 'plant nutrient content', simulation models

Introduction

Production functions

Any production process is characterized by input–output relations. This paper deals with the relation between the input of one or more nutrients and the resulting crop production. Well known – almost classical – forms of input–output relations in the field of crop production are the function of Liebig (or Blackman), associated with the 'law of the minimum' and the function of Mitscherlich (also Mitscherlich–Baule), connected with the 'law of constant activity' (Nijland & Schouls, 1997). (Note: throughout this paper we shall refer to 'laws' and 'equations' as 'production functions'.) Different authors have proposed functions that are positioned in between the functions of Liebig and Mitscherlich. Paris (1992) presents a hybrid function that combines the concepts of Mitscherlich and Liebig, giving a truncated non-linear Liebig function.

Liebscher (1895) proposed a theory that may now be regarded as an early synthesis of the concepts of Liebig and Mitscherlich. More recently, Greenwood *et al.* (1971) and Nijland & Schouls (1997) presented the 'Greenwood variant of Michaelis–Menten's function' (M–M function) as a formalization of 'Liebscher's law of the optimum'. A suggestion for a more fundamental theoretical and mathematical integration of the different functions came from De Wit (1992a, b). He developed a theoretical-ecological synthesis in his last papers as well as in vivid discussions, and in a first version of a new paper that regrettably was never published. In the framework of the question if and when increasing or decreasing marginal productions occur in agriculture, De Wit breathed new life into the more than 100-years-old discussion on production functions. He proposed that 'Mitscherlich', 'Liebscher' and 'Liebig' could be considered as special variants of one system dynamics model, in which it is just a matter of changing one parameter value to produce the different model variants. By elaborating the manuscript that we inherited from De Wit we have been able to confirm his approach and add some other concepts to the model.

Research questions

Our study comprised two research questions: (1) Is it possible – and how – to integrate different well-known production functions within the theoretical framework of one 'integrated model'? and (2) Do some of the discussed variants of the 'integrated model' give rise – and under what conditions – to 'increasing marginal returns'?

Outline of the paper

We start with the elaboration of the 'integrated model', using a sketch of Liebig's function, as it is the most elementary production function. Next we explain why most empirical production curves depart from this simple truncated linear function. Then, we present the more versatile Michaelis–Menten (M–M) function and extend it with the concept of multiplicative interaction, providing a bridge to the 'negative exponential Mitscherlich function'. By mathematical analysis we derive some of the model features. For deduction of the more complicated features the model was

implemented as a system dynamics simulation model. Several runs were done to demonstrate its behavioural variants. Via trial-and-error simulation runs the model was fitted to different empirical datasets and compared with these data by subjective visual inspection. In a final discussion a summary of the paper is given, conclusions are drawn and possible further research is suggested.

Overall structure of the model

In the 'integrated model' (see Figure 1 for an overview) nutrients, nitrogen (N) and phosphorus (P), are taken up and become part of the plant biomass. Paramount in this model is the variable 'stock of available nutrients' (in this paper nutrient stock is synonymous with 'nutrient level' and with 'nutrient concentration', expressed as g of nutrient per m^2 of land area). The nutrient stock is changed by three processes: (1) nutrient supply (either by the farmer or from other sources), (2) nutrient uptake (by the crop), and (3) nutrient loss (to the environment or to other sinks). Nutrient supply is assumed to be an exogenous input variable. Nutrient uptake – and with it dry matter production – is assumed to increase with increasing soil nutrient stock. The form of this relation is specified in the 'basic production function', which we assume to be a Michaelis–Menten function. Also nutrient loss increases with increasing soil nutrient stock according to the 'basic nutrient loss function'. This function may have different

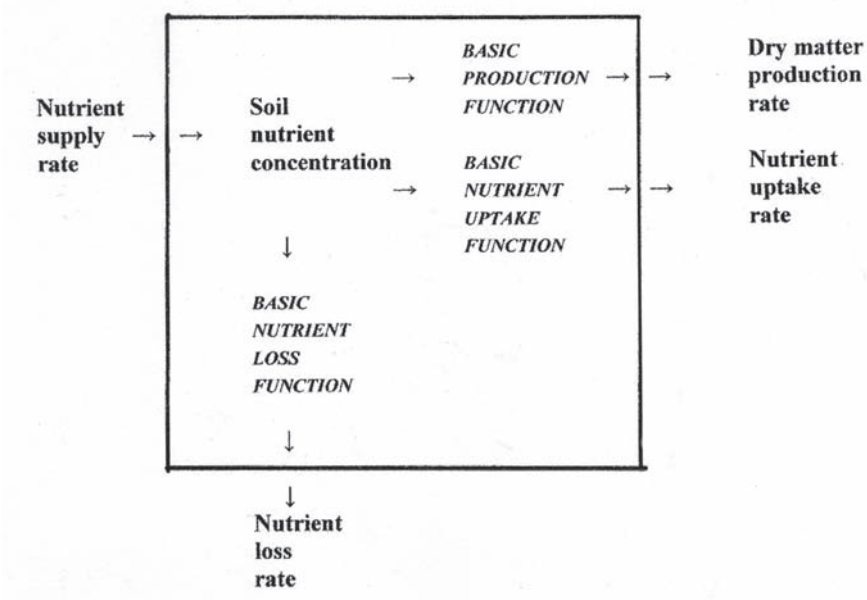

Figure 1. Overall structure of the integrated model. The basic production function and the basic nutrient uptake function within the box are formulated by the Michaelis–Menten function. The relation between *nutrient supply rate* and *production rate* yields the output function of the integrated model.

forms, but in our study we assume a simple linear relationship: 'nutrient loss per day' = 'nutrient stock in the soil' × 'fraction loss per day'. The interaction between these processes determines the overall response of crop growth to nutrient input. Figure 1 shows the overall structure of this 'integrated model'.

Liebig's production function as 'archetype'

Linear response in Liebig's function

Several factors influence plant production. For unrestricted growth the various necessary factors should all be available at a non-limiting rate. The starting point of this paper is the simplification formulated by Liebig. His concept implies that at any moment there is only one factor that limits production. This factor is said to be in minimum supply. If its supply is increased, production will increase proportionally up to a point where a second factor gets into minimum supply and in turn limits production. In Liebig's function the transition of limitation from one factor to the next is an abrupt one, as depicted in Figure 2A.

Before we discuss how to model interactions of different factors, we shall first have a closer look at the response to a single factor, for instance the response of plant production to uptake of soil nitrogen. At this point it is useful to introduce some symbols that will be used throughout this paper; for a complete list of symbols see Appendix 1. Soil nitrogen is symbolized by N_{sol} (the amount of nitrogen in the soil solution, in g per m²) and production rate by r (the rate of dry matter production, in g per m² per day). This production rate has a climatically determined maximum, r_{max}, called the potential production rate (De Wit, 1994). The parameter r_{max} has a value of about 20 g of plant dry matter per m² of soil surface per day. For simplification purposes, 'plant nitrogen content', n, is assumed to be constant at a value of 0.02 g nitrogen per g of DM. Now, if there are no losses, Liebig's function of the plant production rate in terms of nitrogen supply rate, S_N, is given by the following equation:

$$r = \min\,(r_{max}\,,\ S_N\ /\ n) \qquad (1)$$

where S_N is expressed in g per m² per day.

When r is plotted against S_N, the production function shows as a 'broken stick' (Figure 2A). The production rate increases linearly with increasing S_N of the limiting factor nitrogen until a transition point is reached (the obtuse angle in Figure 2A). Increasing S_N beyond this transition point has no effect on the production rate. The production rate is now limited by shortage of the second nutrient (here P), or eventually by climatic factors such as radiation, even if soil factors like other nutrients and water are fully available. For the given parameter values, the transition point for nitrogen limitation is situated at a supply rate of $r_{max} \times n = 0.4$ g of nitrogen per m² per day. The function may be generalized for multiple nutrients, for example for nitrogen (N) and phosphorus (P), as shown by the following equation:

$$r = \min\,(r_{max}\,,\ S_N\ /\ n\ ,\ S_P\ /\ p) \qquad (2)$$

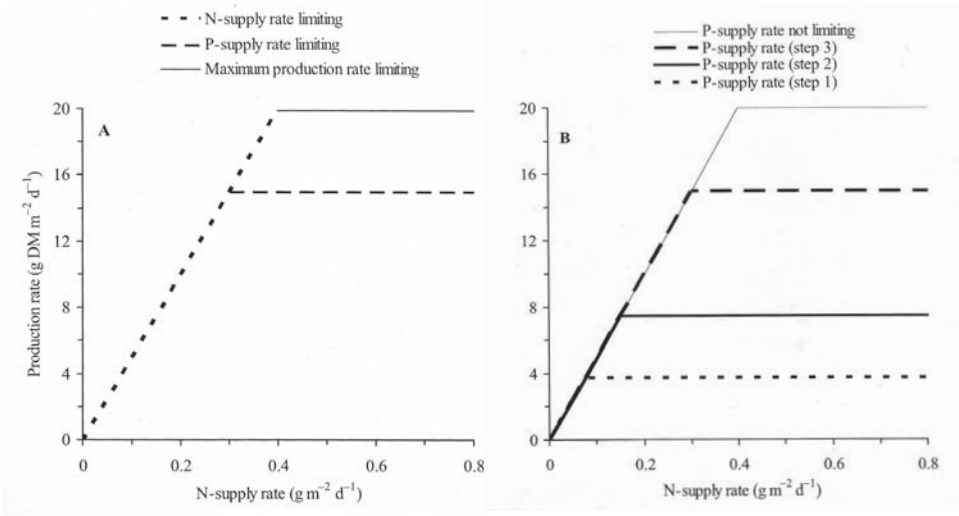

Figure 2.

A: The Liebig production function with respect to nitrogen, at one (limiting) rate of phosphorus supply and at maximum production, i.e., nitrogen and phosphorus not limiting. Parameter values: r_{max} = 20; n = 0.02; p = 0.002; S_P= 0.03.

B: The Liebig production function for three steps of P-supply rate. Parameter values: r_{max} = 20; n = 0.02; p = 0.002; S_P step 1 = 0.0075; S_P step 2 = 0.015; S_P step 3 = 0.03.

This generalized Liebig function is shown in Figure 2B, in which the relation between r and S_N is plotted for three phosphorus supply rates, S_P.

Comparison with gradual saturation curves in practice

The instantaneous response of production to nutrient supply can hardly be measured experimentally. In practice, the plants will be harvested at the end of a much longer production period, so that the response must be determined in terms of accumulated dry matter versus total nutrients – either taken up or applied, or even as initial soil stock. This means that Equation 1 should be rewritten in the form of a time integral. The abrupt Liebig type of transition will be retained only if the production rate and the nutrient supply rate remain constant during this longer period. However, usually the maximum production rate will vary from day to day, due to weather fluctuations, so that production may, for example, be nutrient-limited on a clear day but radiation-limited on a cloudy day. As a result, the response of accumulated plant dry matter to nutrient supply over that period will not be characterized by a sudden saturation, but by a more gradual one (Nijland, 1994; Whitmore & Van Noordwijk, 1995; Nijland & Schouls, 1997). At high nutrient supply rates plant dry matter will become equal to r_{max} accumulated over time. At low nutrient supply rates it will be proportional to the accumulated nutrient uptake over time divided by 'plant nutrient content', n (the mass fraction of N in the dry matter). By similar reasoning, spatial variability will also lead to

a less abrupt saturation of the response curve. Indeed, in practice, a gradual saturation is more common than an abrupt one.

Components of the 'integrated model'

The Michaelis–Menten function

Searching the literature for an acceptable mathematical function of a gradual convex production curve, the Michaelis–Menten (M–M) function appeared to be one of the most frequently adopted. This function, which was originally developed in chemistry, is as follows:

$$V = V_{max} \times C \,/\, (K + C) \qquad (3)$$

where V_{max} is the maximum reaction rate, C the concentration of the limiting compound, and K the M–M constant.

In our field of interest, i.e., plant production, the maximum reaction rate, V_{max}, is the potential production rate, r_{max}, and the concentration of the limiting compound, C, is the nitrogen concentration of the soil, N_{sol}, here taken as the available nitrogen per m^2 in the soil solution. The M–M constant, K, can also be written as r_{max} divided by the affinity for nitrogen, α_N. Analogous to the custom in chemical reactions we may define the affinity coefficient here as the production rate per unit nitrogen when nitrogen is almost 0. It has the unit of (gDM gN^{-1} d^{-1}). The resulting function for production will then prove to be similar to the chemical reaction in Equation 3, which in terms of plant production is represented by the following equation:

$$r = r_{max} \times N_{sol} \,/\, (r_{max} \,/\, \alpha_N + N_{sol}) \qquad (4)$$

The graphical image of this production function is depicted in Figure 3A. It is the simplest M–M production function for one nutrient with maximum production rate, r_{max}. At a low nitrogen supply rate, r approaches $\alpha_N \times N_{sol}$, which means that the nitrogen uptake rate, r_N (nitrogen uptake by the crop in g per m^2 per day), is then equal to $n \times \alpha_N \times N_{sol}$. If there are no losses, the supply rate will be equal to this value. Comparing the curves in Figure 3A with the curve for the Liebig function in Figure 2A we see that their slopes at very low nitrogen supply rates and their maxima at high nitrogen supply rates are the same. At intermediate values the production rate in the M–M equation is lower. In particular, at the transition point, $r_{max} \times n$, the production rate has a value of 50% of the maximum rate (Figure 3A). If we write Equation 4 in its reciprocal form the following equation is derived:

$$1 \,/\, r = 1 \,/\, r_{max} + 1 \,/\, (\alpha_N \times N_{sol}) \qquad (5)$$

This form of representation of the function has its own merits. The first one is that generalization for two or more nutrients gives a convenient arrangement of the terms

for the different nutrients. Later on we shall see that also multiplicative interactions between nutrients can be conveniently added to this function. Generalization for the two nutrients nitrogen and phosphorus gives:

$$1 / r = 1 / r_{max} + 1 / (\alpha_N \times N_{sol}) + 1 / (\alpha_P \times P_{sol}) \qquad (6)$$

Equation 6 represents the 'Greenwood variant of the M–M production function'. Figure 3B is the normal representation of this function, in which the production rate, r, is plotted against the soil nitrogen concentration, N_{sol}, for three constant levels of soil phosphorus concentration, P_{sol}, and also for the condition that phosphorus does not limit production (the upper curve). If plotted reciprocally ($1 / r$ against $1 / N_{sol}$) a set of parallel straight lines with upward slope, $1 / \alpha_N$, is obtained for different P_{sol} levels. Here we have a second advantage of reciprocal representation: it offers the possibility to estimate the parameter values α, α_P and r_{max} by linear regression, if 'Michaelis–Menten' applies, or test any other production curve on possible deviation from the 'Greenwood variant of the M–M function' (Nijland & Schouls, 1997; Kho, 2000). In the normal representation of 'Greenwood' (Figure 3B), the 'law of diminishing marginal returns' can be observed. The slopes of the curves in the origin are the same for all variants with different phosphorus supply rates. The curves are diverging at a higher nitrogen supply rate. The absence of an interaction term does definitely not imply that there is no interaction effect.

'Abruptness of the bending'

The transition from the increasing part of the curve to its saturated maximum will be referred to as *the bending* of the production function. This transition may be gradual, as in the M–M function, or abrupt, as in the Liebig function (Figure 3A). So the 'abruptness of the bending' is different for the two production functions discussed in the foregoing.

This brings us to the question of the mechanism that underlies the bending of the curve becoming more abrupt or pointed, or becoming more gradual. One such mechanism is the variation in diffusion rate between soil-bound nutrients and nutrients in the soil solution. A very low diffusion rate means a very low nutrient supply rate to the plant. As a result, plant demand exceeds supply, the concentration at the site of uptake becomes almost 0 and the rate of uptake will be virtually equal to the supply rate. This situation is known to exist for nitrogen uptake by roots, especially because nitrogen is taken up at an extremely high affinity.

The limitation of the uptake rate by the supply rate requires an equation additional to Equation 4 to represent the nitrogen balance in the soil solution. The nitrogen uptake rate, r_N, is the product of the production rate, r, and 'plant nitrogen content', n. In addition, the losses to the environment have to be accounted for. To this end we lump the effects of all possible losses into one parameter, the relative loss rate of nitrogen, λ_N, representing the fraction of the soil nitrogen in solution (N_{sol}) that is lost daily. The equation for the balance between uptake rate, supply rate and loss rate now becomes:

$$r \times n = S_N - N_{sol} \times \lambda_N \qquad (7)$$

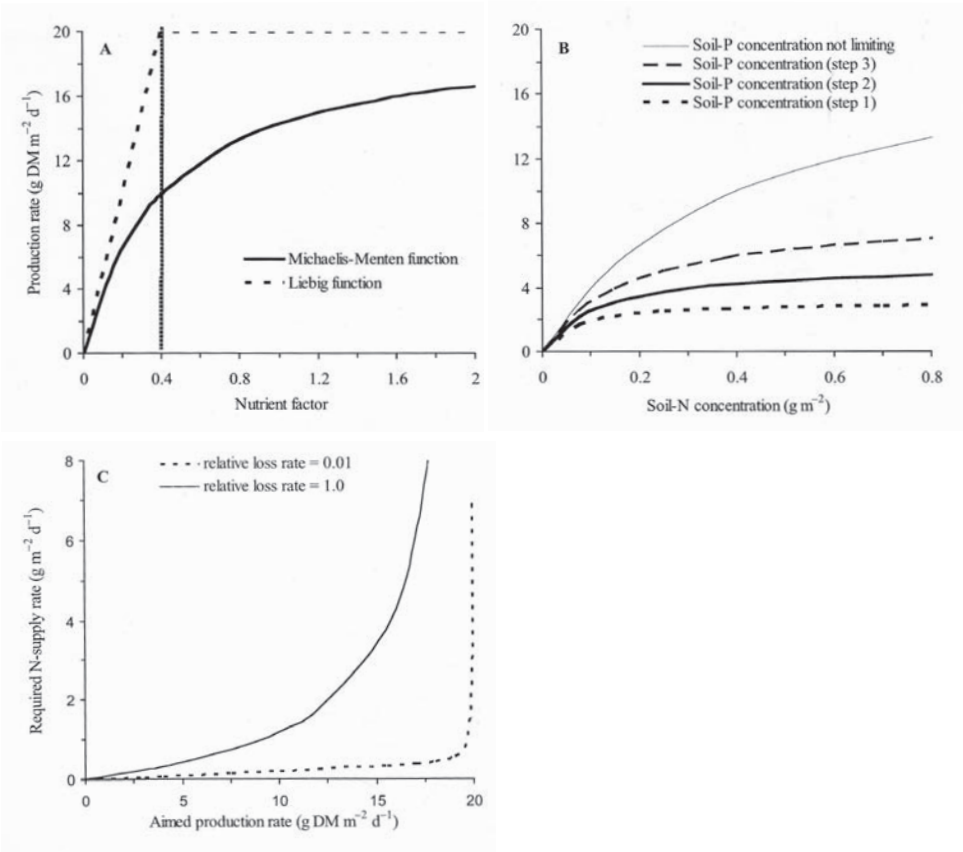

Figure 3.

A: The Michaelis–Menten production function compared with the Liebig function with nitrogen as the only limiting nutrient. Parameter values: $r_{max} = 20$; $\alpha_N = 50$. The nutrient factor on the X-axis is N_{sol} for the M–M function and S_N for the Liebig function. The scale for Liebig's 'basic production function'(r against S_N) may be transformed into the scale for the M–M function (r against N_{sol}) by dividing the Liebig scale by a factor $\alpha_N \times n$.

B: The Michaelis–Menten production function for three steps of soil-P concentration. Parameter values: $r_{max} = 20$; $\alpha_N = 50$; $\alpha_P = 500$; P_{sol} step 1 = 0.0075; P_{sol} step 2 = 0.015; P_{sol} step 3 = 0.03.

C: Required N supply rate, S_N, as a function of the production rate, r, for the Michaelis–Menten basic production function, for values of the parameter λ_N of 0.01 and 1.0. Other parameter values: $\alpha_N = 20$; $r_{max} = 20$; $n = 0.02$.

Equation 7 is combined with Equation 4 by eliminating the local nitrogen concentration in the soil solution, N_{sol}. Substituting $N_{sol} = (S_N - r \times n) / \lambda_N$ from Equation 7 into Equation 4 and taking S_N explicit gives:

$$S_N = r \times [n + (\lambda_N \times r_{max}) / \alpha_N \times (r_{max} - r)] \qquad (8)$$

Because of $(r_{max} - r)$ in the denominator we immediately see that very large values of S_N are required to reach a production rate close to r_{max}. On the other hand, for very

small values of r the supply rate approaches:

$$S_N = r \times n \times [1 + \lambda_N \ / \ (\alpha_N \times n)] \qquad (9)$$

This linear function in r also shows how the loss parameter λ_N increases the required supply rate, even if the production rate is very small. In Figure 3C the required supply rate, S_N, is plotted as a function of the production rate, r. From this it appears that with a low as well as a high relative loss rate λ_N, the same maximum growth rate will be reached but that with a high λ_N the rate of approach is much more gradual. In fact, Equation 9 represents the tangent in the origin of the curve of Equation 8. The latter is a non-rectangular hyperbola in r. Equation 8 furthermore shows that the parameters α_N and λ_N only occur as their ratio. In addition, as the quotient $(\alpha_N \times n) / \lambda_N$ is dimensionless it is useful to substitute it by a new dimensionless parameter φ_N that is defined as follows:

$$\varphi_N = (\alpha_N \times n) / \lambda_N \qquad (10)$$

In Figure 3C we have seen that the expression of S_N as a function of r turns out to be more elegant and more suitable for the demonstration of some of its characteristics than the reverse function, which has production rate as a function of supply rate. Yet, we have to return to this more common input–output relationship, as the M–M function and the Liebig function are written in this form. In case of a very large relative loss rate, λ_N, we may rewrite Equation 8 in the following way, expressing the production rate as a function of supply rate:

$$r = r_{max} \times \alpha_N \times S_N / [\alpha_N \times S_N + (\lambda_N + \alpha_N \times n) \times r_{max}] \qquad (11)$$

This expression is a normal rectangular hyperbola, just like the M–M function represented by Equation 5. It is even identical to this equation, as the soil nitrogen balance requires that the sum of loss rate and uptake rate is equal to the nitrogen supply rate. So the equilibrium soil nitrogen concentration, N_{sol}, will be equal to $S_N / (\lambda_N + \alpha_N \times n)$, and substitution of this expression for N_{sol} in Equation 5 shows that we obtain Equation 11 again. The production rate in Equation 11 will eventually reach the maximum value, r_{max}, for very large values of the nitrogen supply rate. The 50% point of Equation 11 is reached when the nitrogen supply rate is equal to $(\lambda_N + \alpha_N \times n) \times r_{max} / \alpha_N$.

The question now is how to represent situations intermediate between the M–M function and the Liebig function. By dimensionless representation we can easily compare the production functions for different parameter sets, even though the absolute values may be different. For instance, growth rate r, which ranges between 0 and maximum growth rate, r_{max}, can be plotted on a relative scale from 0 to 1 if we define a dimensionless output variable y as:

$$y = r \ / \ r_{max} \qquad (12)$$

In Equation 8 the required supply rate S_N (the input) was given as a function of

the growth rate r (the output). Replacing r / r_{max} by γ and ($\alpha_N \times n$) / λ_N by φ_N we can rewrite this equation as:

$$S_N / (n \times r_{max}) = \gamma \times [1 + 1 / (\varphi_N \times (1 - \gamma))] \quad (13)$$

Now S_N should be scaled as well. At maximum growth rate the nutrient uptake rate is equal to $n \times r_{max}$. This maximum uptake rate will be part of the scaling of S_N, but the loss rate should also be taken into account. Even at a very low supply rate, the ratio of loss over uptake is at least equal to the inverse of φ_N, as shown in Equation 10. Therefore the scaling factor for S_N will be given by $n \times r_{max} \times (1 + 1 / \varphi_N)$, and the dimensionless x-variable will be defined as:

$$x = S_N / [n \times r_{max} \times (1 + 1 / \varphi_N)] \quad (14)$$

Using this definition of x, Equation 13 can be rewritten as follows:

$$x \times (1 + 1 / \varphi_N) = \gamma \times [1 + 1 / (\varphi_N \times (1 - \gamma))] \quad (15)$$

Equation 15 yields a normal second order equation in γ:

$$\gamma^2 / (1 + 1 / \varphi_N) - \gamma \times (1 + x) + x = 0 \quad (16)$$

For all values of φ_N between 0 and infinity, the solution for γ ranges between the 'broken stick' expression by min(x , 1) for the Liebig function and the hyperbolic expression x / (1 + x) (Figure 4). For very large values of φ_N (almost no losses) we almost have a Liebig function with an abrupt bending at x = 1. As losses increase and thereby the value of φ_N decreases, the bending becomes more gradual so that eventually the M–M function is approached.

The parameter φ_N is a measure of the 'abruptness of the bending' of the production function. As long as the considered nutrient is still the major production-limiting factor, φ_N represents also the maximum uptake / loss ratio of the production system. If extended for two or more nutrients the parameter is more complicated than the simple expression $\alpha_N \times n$ / λ_N for one nutrient.

The Mitscherlich function

The M–M function is a rectangular hyperbola in which the maximum is approached gradually. There are other functions that also have a gradual approach of the maximum. One of them is the Mitscherlich function. However, the theoretical idea behind it is different from that of M–M function. The idea behind Mitscherlich is that the relative decrease of the remaining gap between actual and maximum production remains the same for each subsequent unit of nutrient uptake. In the literature this constant relative decrease of the remaining gap ($r_{max} - r$) per unit of increasing growth factor is referred to as the 'law of constant activity' (Humphrey, 1997), which can be expressed by the following differential equation:

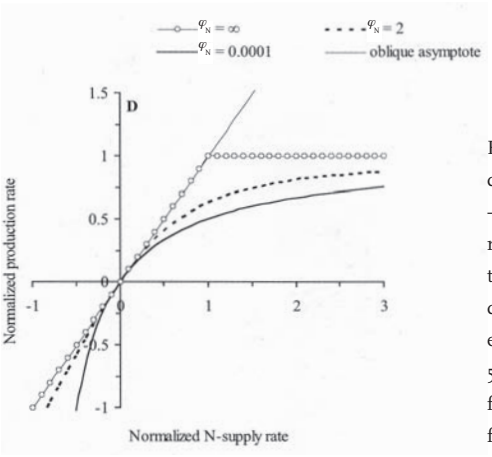

Figure 4. Representation of the 'M–M basic production function' as a non-rectangular hyperbola – the nutrient supply rate and the production rate being normalized at reference value 1, and the model parameters being summarized in one dimensionless parameter φ_N. The parameter φ_N equals $\alpha_N \times n / \lambda_N$. Note: The production rate is 50% of its maximum, at reference value $x = 1$, for φ_N approaching zero (in this figure the curve for $\varphi_N = 0.0001$).

$$dr / dN_{sol} = \alpha_N / r_{max} \times (r_{max} - r) \quad (17)$$

where dN_{sol} represents the relative decrease of the remaining gap, $(r_{max} - r)$.

Integration over N_{sol} leads to a negative exponential function:

$$r = r_{max} \times [1 - \exp(-\alpha_N \times N_{sol} / r_{max})] \quad (18)$$

The corresponding production function of Mitscherlich is shown in Figure 5A (upper curve). If properly parameterized, the curve of Equation 18 has the same initial slope and the same maximum as the M–M function and Liebig's function, but an 'abruptness of the bending' that is intermediate between 'Liebig' and 'M–M'. At the transition point, where $N_{sol} = r_{max} / \alpha_N$, the production rate, r, has a value of 63% of the maximum. So the maximum is approached more rapidly than in the 'M–M' of Figure 3A. The 'hyperbolic M–M function' and the 'negative exponential Mitscherlich function' are mechanistically different, but 'M–M' can be mathematically transformed into 'Mitscherlich' by an exponential transformation of the independent co-ordinate of 'M–M' (Goudriaan, 1979).

Co-limitation and interaction by two nutrients

We shall now extend the theory for limitation by one nutrient to the simultaneous limitation by two nutrients, nitrogen and phosphorus. The Mitscherlich function can be extended for describing co-limitation by two nutrients, simply by multiplying the expression by another negative exponential factor for the second nutrient:

$$r = r_{max} \times [1 - \exp(-\alpha_N \times N_{sol} / r_{max})] \times [1 - \exp(-\alpha_P \times P_{sol} / r_{max})] \quad (19)$$

The graphic representation of Equation 19 is given in Figure 5B – here again for three constant levels of soil phosphorus concentration. The part $r_{max} \times [1 - \exp(-\alpha_P$

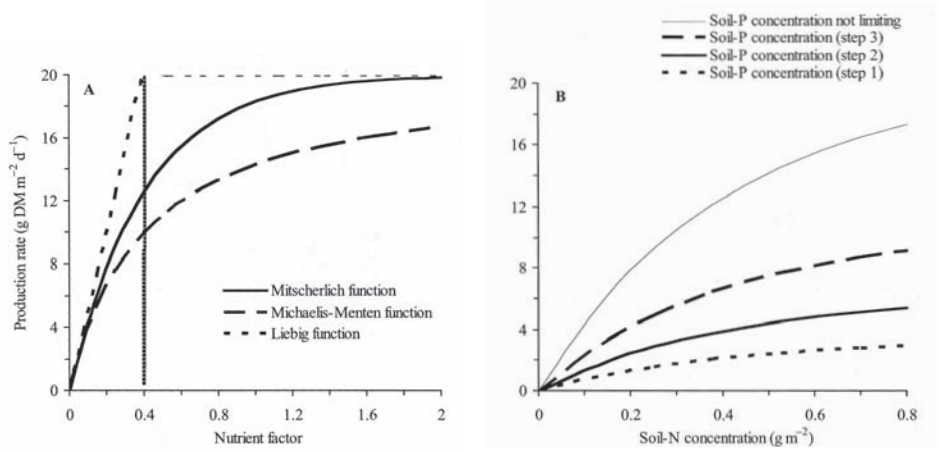

Figure 5.
A: The Mitscherlich production function compared with the Michaelis–Menten and the Liebig functions with nitrogen as the only limiting nutrient. Parameter values: r_{max} = 20; α_N = 50. The nutrient factor on the X-axis is N_{sol} for the Mitscherlich function (and for the M–M function) and S_N for the Liebig function. The scale for Liebig's function'(r against S_N) may be transformed into the scale for the other variants (r against N_{sol}) by dividing the Liebig scale by a factor $\alpha_N \times n$.
B: The Mitscherlich production function for three steps of soil-P concentration. Parameter values: r_{max} = 20; α_N = 50; P_{sol} step 1 = 0.0075; P_{sol} step 2 = 0.015; P_{sol} step 3 = 0.03.

$\times P_{sol} / r_{max})]$ will act as a maximum in the response function to nitrogen. For small values of both nutrients the equation approaches a multiplication of their effects, resulting in $\alpha_N \times \alpha_P \times N_{sol} \times P_{sol} / r_{max}$. This explains why the Mitscherlich function is often identified with multiplicative interaction of the effects of the different limiting factors, more so than the other production functions. However, the following equation shows that there is no reason why the interaction between two limiting nutrients could not be formulated with the M–M function:

$$r = r_{max} \times [N_{sol} / (r_{max} / \alpha_N + N_{sol})] \times [P_{sol} / (r_{max} / \alpha_P + P_{sol})] \qquad (20)$$

In its reciprocal form this equation will read as follows:

$$1 / r = 1 / r_{max} + 1 / (\alpha_N \times N_{sol}) + 1 / (\alpha_P \times P_{sol}) + r_{max} / (\alpha_N \times \alpha_P \times N_{sol} \times P_{sol}) \qquad (21)$$

This shows that the reciprocal of r consists of the sum of four terms of which the fourth one contains the product of the two nutrients. Generalizing the strength of the interaction to a dimensionless parameter α_{NP}, we may rewrite Equation 21 as:

$$1 / r = 1/r_{max} + 1/(\alpha_N \times N_{sol}) + 1/(\alpha_P \times P_{sol}) + 1/(\alpha_{NP} \times N_{sol} \times P_{sol}) \qquad (22)$$

where α_{NP} is a measure for the extra response of production to the combination of

nitrogen and phosphorus – apart from the separate responses α_N and α_P to these nutrients. Equations 21 and 22 – for being identical – require the parameter α_{NP} to be equal to $\alpha_N \times \alpha_P / r_{max}$. The variant is represented in Figure 5B. For only an increase in the nitrogen supply rate (other nutrients constant) the feature of 'diminishing marginal returns' applies. This means that each subsequent unit of supply yields less. For an increase in both nitrogen supply rate and other nutrients in proportion, the marginal returns first increase and then decrease: starting at 0 each subsequent unit yields more until a certain rate from where each subsequent unit yields less.

Responsive 'plant nutrient content'

In this paper we have assumed constant 'plant nutrient contents', n and p. In reality plants are able to adapt their nutrient content to the nutrient supply, and a range of a factor 4 between minimum and maximum nutrient content is not uncommon. For instance, the minimum and maximum nitrogen contents might well be 1% and 4%, respectively, instead of the constant value of 2%, and similarly, the phosphorus content could vary between 0.1% and 0.4%, respectively, instead of being constant at 0.2%. It is possible to model this adaptation by multiplying the nutrient affinities by minimum and maximum 'plant nutrient content', ensuring that nutrient content responds such that a minimum nutrient content occurs at very low nutrient supply rates, and a maximum content at very high nutrient supply rates according to the following equations:

$$1/r_N = 1/ (n_{max} \times r_{max}) + 1/(\alpha_N \times n_{min} \times N_{sol}) + 1/(\alpha_P \times n_{max} \times P_{sol}) + 1/(\alpha_{NP} \times n_{min} \times N_{sol} \times P_{sol}) \quad (23)$$

$$1/r_P = 1/(P_{max} \times r_{max}) + 1 /(\alpha_P \times P_{min} \times P_{sol}) + 1/(\alpha_N \times P_{max} \times N_{sol}) + 1/(\alpha_{NP} \times P_{min} \times P_{sol} \times N_{sol}) \quad (24)$$

In this way the dry matter production rate is still the same as in Equation 22, but the nutrient uptake rates (Equations 23 and 24) at low nutrient supply are lower and at high nutrient supply higher than before. Note that the uptake equation for nitrogen when phosphorus is non-limiting is given by the following equation:

$$1 / r_N = 1 / (n_{max} \times r_{max}) + 1 / (\alpha_N \times n_{min} \times N_{sol}) \quad (25)$$

Introducing the mechanism of responsive 'plant nutrient content' makes the linear slopes of a 'Liebig variant' non-linear, comparable to the model of Paris (1992).

Implementation as a system dynamics simulation model

The differential equation for soil nutrient concentration

Let us consider both nitrogen uptake by roots as well as subsequent plant production as if they were chemical reactions originally described by the M–M function (Equation

5). The amount of nitrogen in the soil solution, N_{sol}, is a systems state variable. On the one hand it decreases by losses to the environment, $\lambda_N \times N_{sol}$, and by nitrogen uptake, r_N. On the other hand it increases with nitrogen supply, S_N, (fertilization) or from an external stock, N_{ext} (mineralization and the like). The net change rate of nitrogen in the soil solution, dN_{sol} / dt, is given by the following equation, i.e., no longer assuming that the rates are in balance:

$$dN_{sol} / dt = S_N - r_N - \lambda_N \times N_{sol} \quad (26)$$

Equation 26 shows that the loss parameter, λ_N, must have the dimension of the inverse of time. We may interpret this parameter as the fraction of the dissolved nitrogen in the soil solution lost to the environment per unit of time. Expressed in terms of the local soil nitrogen concentration, N_{sol}, the production function is still in the form of the M–M function (Equation 5). As we showed in the foregoing, the transition to the Liebig function can only occur at the response of production rate to supply rate, rather than at the response to soil nitrogen concentration. If the losses to the environment are almost nil, all of the nutrient will be taken up (linear response of production rate to supply rate) or the nitrogen supply will be in excess of demand and the remainder will accumulate in the soil (maximum production rate). At the transition point of the 'broken stick' the supply rate precisely meets the demand (Figures 2A and 2B). It is, however, possible to rewrite Equation 26 into a form that has an external *concentration* at the input side, rather than a *supply rate*. We define a virtual external concentration, N_{ext}, and an apparent diffusion rate, ε_N, such that the supply rate is equal to $(N_{ext} - N_{sol}) \times \varepsilon_N$. Equation 26 can then be written as:

$$dN_{sol} / dt = (N_{ext} - N_{sol}) \times \varepsilon_N - r_N - \lambda_N \times N_{sol} \quad (27)$$

The merit of this equation is that it provides a mechanism for the transition between the different response curves, close to the original idea of De Wit (unpublished manuscript). He envisioned a replenishment rate of a 'reaction vessel' with an inflow of solute with nutrients and an outflow with unused nutrients and synthesized product. Now the term $(N_{ext} - N_{sol}) \times \varepsilon_N$ stands for the daily replenishment rate. The losses from the whole system are given by the product $\lambda_N \times N_{sol}$. Whether S_N or N_{ext} are considered as independent variables or not, all transitions between the M–M and the Liebig functions that we presented in the foregoing remain possible.

However, we used two parameters (N_{ext} and ε_N) to replace a single one, S_N, which means that one is redundant. As far as the dimensionless parameter $\varphi_N = (\alpha_N \times n) / \lambda_N$ (Equation 10) is concerned, ε_N should be added to λ_N to establish their combined effect on the 'abruptness of the bending'. So it is best to omit the return flow $N_{sol} \times \varepsilon_N$, and rewrite Equation 27 as:

$$dN_{sol} / dt = \lambda_N \times N_{ext} - r_N - \lambda_N \times N_{sol} \quad (28)$$

It is immaterial whether the disappearing nutrient flows to the infinite sink of the environment or back to the also infinite source of the soil nutrient stock. In both

cases the nutrient has left the rooting zone and its environment, and has no relevance to the model behaviour. Which of the Equations 26 and 28 is to be preferred depends on whether the supply is formulated in terms of concentration of the external source (Equation 28) or in terms of an imposed supply rate (Equation 26).

Simulation techniques

Different methods may be used to implement the equations presented in the foregoing. As long as only one or two nutrients are involved it is possible to implement the model as an analytical mathematical model. But with three or more nutrients or when the model becomes otherwise more complicated, implementation as a numerical simulation model is the only possibility left. Which simulation method is best will also depend on the previous training and experience of the user. Popular simulation tools are available in Fortran, CSMP, DYNAMO, FST, MATHLAB, but also Excel can be used. For the methodology of simulation with system dynamic models we refer to De Wit & Goudriaan (1978) and Richardson & Pugh (1981).

Rather than finding the model behaviour over time, our aim of this simulation was to find the relations between the variables at any time at which the model is in equilibrium. The relations between the equilibrium values of the variables can be found by numerical integration over a period of time long enough to reach equilibrium. The response to a varying soil stock, N_{ext}, or supply rate, S_N, may be found by applying a very slow and gradual increase, slow enough to maintain a quasi-steady state. The uptake rate may then be plotted as a function of the nitrogen supply rate instead of a function of the soil nitrogen concentration. For this procedure the state variable approach of the FST simulation language was used.

Variants of the 'integrated model'

Reproduction of the 'basic functions' from the 'integrated model'

Simulation runs with the 'integrated model' were done to reproduce the 'Full model', the 'Greenwood variant', the 'De Wit variant' and the 'Liebig variant', as well as variants between these ideal-types. The results are graphically presented in the Figures 6A, 6B, 6C and 6D. Depending on the relative value of the parameters α_N, α_P, and α_{NP}, and on r_{max}, various functions can be obtained from the 'basic production function'.

If α_{NP} is equal to $\alpha_N \times \alpha_P / r_{max}$, Equation 21 is a purely multiplicative M–M function (Figure 6A). In this case a change in one nutrient (N) does not affect the M–M constant of the other (P). This function is the 'Full model variant of the M–M function' (Figure 6A), which obviously has features in common with the following ideal-types derived from it.

If α_{NP} is larger than $\alpha_N \times \alpha_P / r_{max}$, the result is a less than multiplicative M–M function. For very large values of α_{NP} the multiplicative term totally disappears and the 'Greenwood variant' is obtained. For this function see Equation 6 and Figure 3B.

On the other hand, if α_{NP} is smaller than $\alpha_N \times \alpha_P / r_{max}$, the interaction between

the nutrients nitrogen and phosphorus is stronger than in the 'Full model variant'. Eventually, when α_N and α_P become very much larger than α_{NP} the function $1 / r = 1/ r_{max} + 1 / (\alpha_{NP} \times N_{sol} \times P_{sol})$ results. If r_{max} is extremely large as well, only the multiplicative term remains, and 'De Wit's multiplicative variant' of the 'basic M–M function' is obtained: $1 / r = 1 / (\alpha_{NP} \times N_{sol} \times P_{sol})$. For this multiplicative M–M variant see Equation 29 and Figure 5B.

Up to this point the functions 'Greenwood', 'De Wit', and 'Full model' could be explained as variants of the 'basic production function' only. For explaining the emergence of the 'Liebig variant', however, system dynamics features of the complete 'integrated model' are required. To understand this, it is appropriate to make a clear distinction between two definitions of the term 'production function': (1) the 'basic production function', which gives the relation between soil *nutrient concentration* and *production rate* at the root level, and (2) the apparent relation between *nutrient supply rate* and *production rate*, at the production system level in the integrated model. This integrated model not only consists of the 'basic production function', but also of a 'basic nutrient loss function'. The feedbacks between these processes are part of it. The diffusion barriers between the nutrient supply, via the soil nutrient concentration, and the nutrient uptake process (directly accessible nutrients in the soil solution) conceptually connect the two definitions of the term 'production function' (1) and (2).

Whether the ideal-typical variants of the 'basic production function' (Figures 3B and 5B) emerge or whether they are shifted more or less into the direction of the 'Liebig variant' depends on the ratio between the *affinity coefficients* on the one hand and the *relative loss rates* on the other. For low affinities and/or high relative loss rates (small φ_N) the Greenwood variant is approached (Figure 6B) and for large φ_N the 'Liebig variant' (Figure 6D). It may be noted that the curve for the highest phosphorus supply step, however, has an imperfect Liebig form.

On the basis of the aforementioned theory the Figures 6D, 6B and 6C are expected to be quite similar in form to the illustrations of the corresponding 'basic production functions' in the Figures 2B, 3B and 5B, respectively. The difference is that the Figures 2B, 3B and 5B are images of the 'basic production function' only, whereas the Figures 6D, 6B and 6C are simulated with the complete 'integrated model' with an extended set of parameters and variables – the added ones being the relative loss rates, λ_N and λ_P. Moreover, the independent variables in the plots are not the soil nutrient concentrations, N_{sol} and P_{sol}, but the nutrient supply rates, S_N and S_P.

Because of the additional parameters, and different parameter values, the simulated curves differ slightly from the images of the corresponding 'basic production functions'. In particular the value of parameter λ_N in the simulation run of Figure 6D has a value 0.01 instead of 0, as required for the 'Liebig ideal-type'. The run of Figure 6B has a value of 1 instead of infinity, as required for 'Greenwood's ideal-type'. The shape of the 'Negative exponential Mitscherlich function' of Figure 5B also differs somewhat from 'De Wit's multiplicative variant' in Figure 6C. However, the overall patterns in the figures are similar, and since the relatively large differences in parameter values (α_N = 20 or 200; α_P = 200 or 500) only give small differences in output, it may become clear that the sensitivity of the model to changes in parameters is still an important subject for further studies.

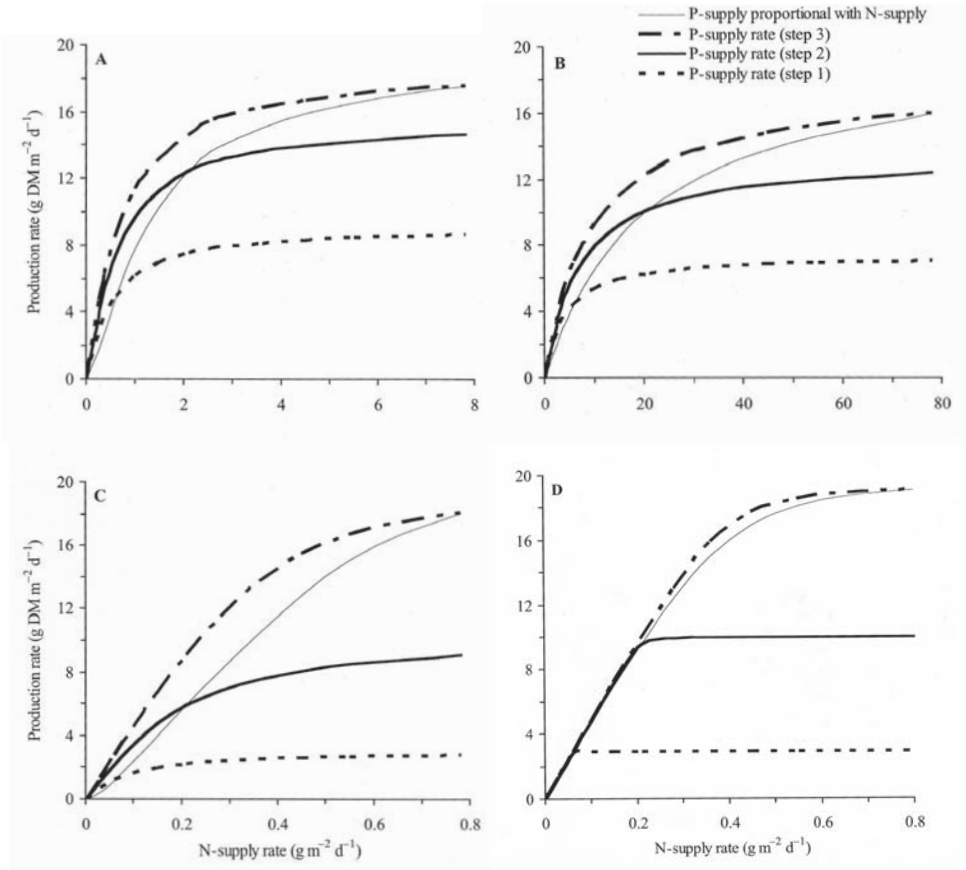

Figure 6.

A: Variant of the integrated model with main terms, interaction term, low values of affinity coefficients and high values of the relative loss rates, as an approximation of the 'Full model' ideal-type. Parameter values: r_{max} = 20; n_{max} = n_{min} = 0.02; p_{max} = p_{min} = 0.002; λ_N = λ_P = 0.50; α_N = 20; α_P = 200; α_{NP} = 200; S_P step 1 = 0.06; S_P step 2 = 0.21; S_P step 3 = 0.78; S_P curve 4 (proportional inputs, S_P = S_N / 10).

B: Variant of the integrated model with only active main terms and low values of affinity coefficients and high values of the relative loss rates, as an approximation of the 'Greenwood ideal-type' (M–M without multiplicative term). Parameter values: r_{max} = 20; n_{max} = n_{min} = 0.02; p_{max} = p_{min} = 0.002; λ_N = λ_P = 1; α_N = 2; α_P = 20; α_{NP} = 999999; S_P step 1 = 0.6; S_P step 2 = 2.1; S_P step 3 = 7.8; S_P curve 4 (proportional inputs, S_P = S_N / 10).

C: Variant of the integrated model with only an active multiplicative interaction term and low value of the interaction coefficient, as an approximation of 'De Wit's multiplicative ideal-type'. Parameter values: r_{max} = 20; n_{max} = n_{min} = 0.02; p_{max} = p_{min} = 0.002; λ_N = λ_P = 0.01; α_N = 999999; α_P = 9999999; α_{NP} = 1; S_P step 1 = 0.006; S_P step 2 = 0.021; S_P step 3 = 0.078; S_P curve 4 (proportional inputs, S_P = S_N / 10).

D: Variant of the integrated model with high values of affinity coefficients and low values of relative loss rates, as an approximation of the Liebig ideal-type. Parameter values: r_{max} = 20; n_{max} = n_{min} = 0.02; p_{max} = p_{min} = 0.002; λ_N = λ_P = 0.01; α_N = 20; α_P = 200; α_{NP} = 999999; S_P step 1 = 0.6; S_P step 2 = 2.1; S_P step 3 = 7.8; S_P curve 4 (proportional inputs, S_P = S_N / 10).

Apart from production, also nutrient loss is an important criterion. In our model the nutrient losses are necessarily equal to the difference between the supply rate and the uptake rate by the crop. So the nutrient loss curve has 'mirror properties' with respect to the production function. This means that the losses will rise more than proportionally beyond the transition point defined by the scaling factor for supply rate, $n \times r_{max} \times (1 + 1 / \varphi_N)$ (see also Equation 14 and Figure 4). The closer the system is to 'Liebig', the smaller the losses will be, but the faster they will rise beyond the transition point. The relative loss per unit of production plotted against proportional supply rate is expected to yield a curve that *increases* more than proportionally. In the 'De Wit' and 'Liebscher' variants with a sigmoid curve (case of proportional N- and P-supply rates), the same 'mirror features' imply that the losses sequentially show a gradual increase, a decline and a strong increase with increasing input (Figure 6C). The local maximum in the loss curve corresponds with the 'increasing upward slope trajectory' of the production function and the local minimum with the 'decreasing upward slope trajectory' (Figure 6C). 'Nutrient loss per unit of production' plotted against proportional supply rates is expected (contrary to 'Liebig' and 'M–M') to yield a curve that gradually descends, until a minimum, beyond which the curve rises again. This agrees with inferences from the same production functions by Nijland & Schouls (1979). So for 'resource use efficiency discussions' it seems relevant whether production functions with, or without (effective) multiplicative terms are applicable.

Increasing or decreasing marginal returns

Rational farmers aim at increasing their fertilizer application rates for different nutrients together in a constant ratio. 'Increasing marginal returns' may result from this.

These 'increasing marginal returns' cannot be expected with the production functions of Liebig and Greenwood, because of the absence of interaction terms. This is clearly illustrated in Figure 6D for the 'Liebig variant' of the 'integrated model', and in Figure 6B for that of Michaelis–Menten. The curves of the production rate plotted against N-supply (with proportional P-supply) are linear for 'Liebig' and show a saturation curve for 'Greenwood', just like the curves of production rate plotted against nitrogen supply (with constant phosphorus supply) in the same figures.

For the variants with a multiplicative interaction term, however, 'increasing marginal returns' are possible. The curve of the production rate plotted against nitrogen supply (with proportional phosphorus supply) then becomes a sigmoid with an inflexion point at a relatively low nitrogen supply (Equation 29 and Figure 6C). The sigmoid can approximately be described by the simple function $y = x^2 / (x^2 + 1)$, in which y represents the normalized production rate, r / r_{max}, and x represents the normalized nitrogen supply rate, $N_{sol} \times \mathrm{sqrt}\,[\alpha_{NP} \times (p / n) / r_{max}]$. The parameter α_{NP} is called the NP interaction affinity coefficient, defined as the degree of increase per unit of P of the production rate per unit of N, for very small N and P. It has the unit of (gDM m^{-2} d^{-1} gN^{-1} gP^{-1}).

So 'increasing marginal returns' are possible only for variants of the M–M model

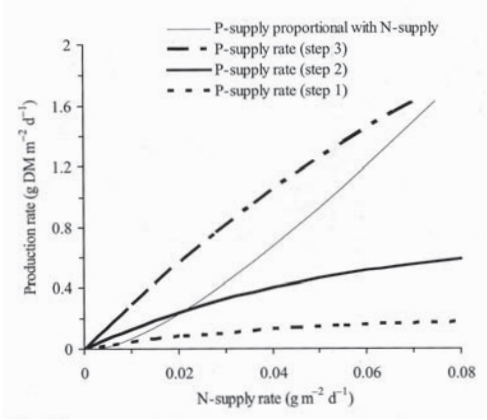

Figure 7. Variant of the integrated model with only one active multiplicative interaction term and low value of the interaction coefficient, as an approximation of 'De Wit's multiplicative ideal-type'. Parameter values: r_{max} = 20; n_{max} = n_{min} = 0.02; p_{max} = p_{min} = 0.002; λ_N = λ_P = 0.01; α_N = 999999; α_P = 9999999; α_{NP} = 1; S_P step 1 = 0.0006; S_P step 2 = 0.0021; S_P step 3 = 0.0078; S_P curve 4 (proportional inputs, S_P = S_N / 10).

with at least some influence of the multiplicative term. Obviously, this effect is stronger for the 'De Wit variant' (multiplicative term only) (Figure 6C) than for the 'Full model variant' (with multiplicative and main terms) (Figure 6A). In Figure 7 we have zoomed in on the feature of 'increasing marginal returns' for the 'De Wit variant'. We shall explain from the model how such 'increasing marginal returns' come about, and under which conditions they disappear. For very small values of the soil nutrient concentrations, N_{sol} and P_{sol}, and the parameter α_{NP}, the dependent variable 1 / r in Equation 22 will be mainly determined by the second order term, 1 / ($\alpha_{NP} \times N_{sol} \times P_{sol}$). Compared with this term the values of the first three terms 1 / r_{max}, 1 / ($\alpha_N \times N_{sol}$) and 1 / ($\alpha_P \times P_{sol}$) may be neglected. Under this condition, Equation 22 simplifies into:

$$1 / r = 1 / (\alpha_{NP} \times N_{sol} \times P_{sol}) \qquad (29)$$

This term is exactly the chemical analogue in De Wit's unpublished manuscript of 1992, because we may rewrite Equation 29 as:

$$r = \alpha_{NP} \times N_{sol} \times P_{sol} \qquad (30)$$

De Wit envisaged two dissolved substances that react and form one new product. If the interaction affinity parameter, α_{NP}, is very small, the reaction in the crop system (De Wit's reaction vessel) proceeds so slowly that the nutrient concentrations, N_{sol} and P_{sol}, in the crop system as well as the production rate, r, become almost proportional to the supply rates, S_N and S_P. At relatively low values of nitrogen supply the marginal production rate increases quadratically with the increase in the nitrogen supply rate, S_N, and the resulting production curve is concave (Figures 6C and 7). These figures show that at higher nitrogen supply rates concavity changes into convexity. If the interaction affinity constant is large (and/or the relative loss rates small), the uptake rate will be limited by the supply rate just as in the case of a single nutrient.

Let us now consider the effect of two nutrients supplied simultaneously in exactly

the required proportion of plant nutrient content, $n : p = 10 : 1$. Equation 29 may then be rewritten as follows:

$$1 / r = [1 / (\alpha_{NP} \times 0.1)] \times (1 / N_{sol}^2) \quad (31)$$

A proportional combination of the nutrient supply rates implies that one nutrient can never become more limiting than the other. Because of this coupling, the combination may be regarded as the supply of one 'compound nutrient', NP, proportional to the corresponding supply rate, S_N (also proportional to N_{sol}, in the case of equilibrium).

From Equation 31 one would expect a quadratic response of r to N_{sol}. As r is proportional to both uptake rates (because of the constant nutrient contents), the soil nitrogen concentration is proportional to the square root of the uptake rate r_N. Furthermore, because the nutrient loss rates are 0, and the system is in steady state, the supply rate, S_N, equals the uptake rate, r_N. All this implies that the soil nitrogen concentration, N_{sol}, increases proportionally with the square root of the supply rate, S_N, and both N_{sol}^2 and r increase linearly with S_N. It becomes clear that if the supply rates, S_N and S_P, are in exactly required proportion, the resulting equilibrium concentrations, N_{sol} and P_{sol}, will be in the same proportion. So if both nutrients happen to be supplied in precisely the required proportion, the outcome is that the concentration of each of the coupled nutrients rises as the square root of its supply rate! This phenomenon explains why at higher values of the interaction affinity coefficient, α_{NP}, the resulting response function tends to become linear over almost its entire range – even in the case of exactly proportional supply rates (compare Figures 6C and 6D).

A high interaction affinity, α_{NP}, is not the only condition for the phenomenon of 'increasing marginal returns' to disappear. Small relative loss rates, λ_N and λ_P, have the same effect. Equation 10 for the 'abruptness of the bending', $\varphi_N = (\alpha_N \times n) / \lambda_N$, shows that a higher value of α_N has the same effect as a lower value of λ_N. Nutrients that disappear due to losses strengthen the phenomenon of 'increasing marginal returns', whereas nutrients that disappear as a result of plant uptake weaken it. The occurrence of 'increasing marginal returns' is also weakened by an increase in spatial soil variability. Finally, the phenomenon weakens accordingly as the proportionality between both nutrients departs more from the harmonious ratio n / p.

The conclusion of this chapter is that the phenomenon of 'increasing marginal returns' is theoretically possible indeed, but only if the affinity constant, α_{NP}, is small (and/or the loss parameters, λ_N and λ_P, are large, and in right proportion too) – situations that occur under severely production-limiting conditions, but these are rare in highly productive agriculture. Under such conditions the effects of the multiplicative interactions vanish. In fact, no production function – irrespective of its mathematical form – can ever surpass the linear asymptotic limits imposed by the supply rates, the 'plant nutrient contents' and the relative loss rates.

Illustration of the 'integrated model' with empirical data

Only a few suitable datasets were found for comparisons with the 'integrated model'.

Especially data for situations with a low nutrient supply and low production are scarce. Moreover, the model has a complex structure that consists of linear and non-linear relations, with feedbacks. Fitting such models to incomplete datasets with unknown distribution probabilities is problematic. Another problem is the large number of parameters involved in the 'integrated model'. Apart from the parameters of our 'integrated model' we could not do without some additional parameters representing the supply rates of nutrients from internal sources.

For the comparison of our model with empirical data we therefore proceeded in a practical way. We do not claim that this procedure provides an empirical validation of the model. We only aim at an illustration of our model. No least square optimization method was used. Instead, we did trial and error experiments with the simulation model, trying to reproduce some datasets.

Our simplification implied that the interaction terms between nutrients were omitted from the model. Furthermore, we started with some imposed *a priori* known parameter values such as r_{max} (20 g m^{-2} d^{-1}), and also imposed reasonable ranges for 'plant nutrient contents' (see the captions of Figures 8A, 8B, 8C and 8D). We tried out simulations with reasonable values for the nutrient affinities and the relative loss rates. The datasets used were from Greenwood *et al.* (1971), Van Heemst *et al.* (1978) and Penning De Vries & Djiteye (1982).

In the Figures 8A, 8B, 8C and 8D the simulated curves are plotted together with the data. In the figures the empirical data are labelled (emp) and the simulated data are labelled (mod). From the figures we conclude that a rather good fit of the model to the data was obtained. Apparently no interaction terms are needed to describe the empirical data. This is in accordance with a statement by Greenwood *et al.* (1971) – citing different other authors – that when using the M–M model in its form of additive combination of reciprocal terms (Equation 22), the main terms suffice to describe the interaction of the nutrients.

The conclusion is that the 'integrated model', without multiplicative interaction terms, suffices to describe these data reasonably well. The implication of the model is that in these data no 'increasing marginal returns' on proportional supply can be demonstrated. The conclusion corroborates earlier observations regarding these data by Nijland & Schouls (1997).

Final discussion and summary

In this paper we have shown that some of the best-known production functions can be theoretically derived from a single 'integrated model'. In this 'integrated model' the Michaelis–Menten function (M–M function) is the 'basic production function' (Equation 6).

The other derived functions may be considered as special cases of the 'basic M–M function'. They can be obtained by just changing one or more parameter values. Transformations can be done by varying: (1) the relative dominance of main terms versus interaction terms in the model, (2) the magnitude and mutual proportions of affinity parameters and relative loss rate parameters of the nutrients, and (3) the degree

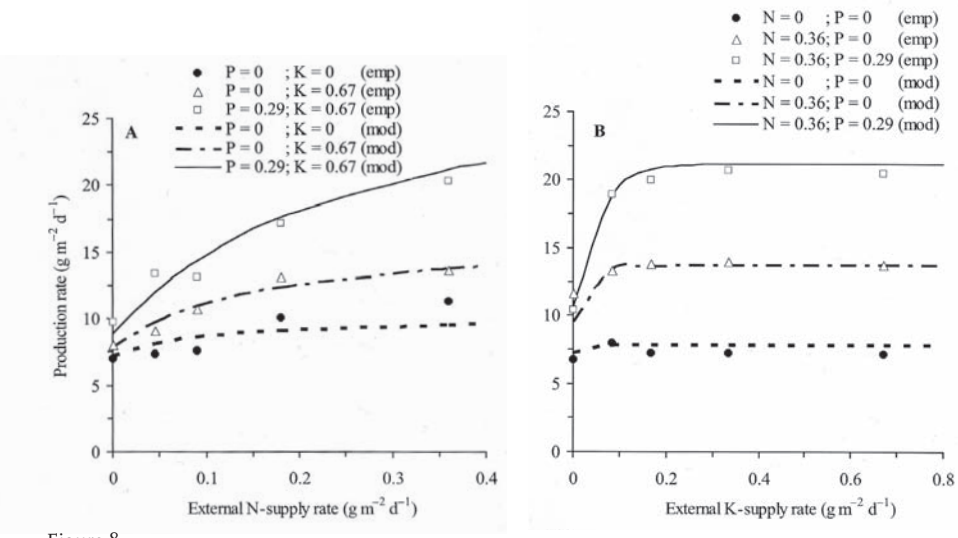

Figure 8.

A: Comparison of the complete model (three nutrients, N, P and K) with empirical data of Greenwood *et al.* (1971). Production rate against external nitrogen supply rate for different constant rates of potassium and phosphorus supply. Crop is French bean (fresh weight); Parameter values: n_{min} = 0.006; n_{max} = 0.030; p_{min} = 0.0005; p_{max} = 0.0025; k_{min} = 0.0015; k_{max} = 0.0030; λ_N = 0.005; λ_P = 0.001; λ_K = 0.003; r_{max} = 30; α_N = 500; α_P = 1000; α_K = 500; α_{NP} = α_{NK} = α_{PK} = α_{NPK} = 9999999; $S_{N\text{-}ext}$ = 0.075; $S_{P\text{-}ext}$ = 0.015; $S_{K\text{-}ext}$ = 0.025; S_N steps = 0.0001 / 0.045 / 0.090 / 0.180 / 0.360; S_P steps = 0.0001 / 0.039 / 0.078 / 0.145 / 0.290; S_K steps = 0.0001 / 0.084 / 0.168 / 0.335 / 0.670. Assuming a growing season of 100 days, 1 g m^{-2} d^{-1} equals 1 ton ha^{-1} year^{-1}.

B: Comparison of the model with empirical data of Greenwood *et al.* (1971). Production rate against external potassium supply rate for different constant rates of nitrogen supply and phosphorus supply (continuation). For parameter values see Figure 8A.

of responsiveness of the 'plant nutrient content' itself.

For the description of the 'integrated model' we started with the M–M function for a single nutrient, nitrogen. This function was compared with the Liebig function, which has the same slope in the origin and the same maximum. The Liebig function, however, has an abrupt bending (broken stick form), whereas the M–M function has a gradual bending. Most empirical production functions are situated between these two and have an intermediate 'abruptness of the bending'. The abruptness depends on the relative loss rate, λ_N, the affinity coefficient of the nutrient, α_N, and the 'plant nutrient content', n. It may be expressed by a function of these three: $\varphi_N = (\alpha_N \times n) / \lambda_N$, in which φ_N is a dimensionless parameter.

Next, the 'basic M–M function' was generalized for two nutrients, nitrogen (N) and phosphorus (P), and extended with a multiplicative interaction term (Equation 22). Depending on the ratios among the affinity parameters α_N, α_P and α_{NP}, the 'basic M–M function' (being the relation between production rate, r, and soil nitrogen concentration, N_{sol}) gets the shape of three different production functions known from the literature: (1) that of Greenwood, (2) that proposed by De Wit in his unpublished

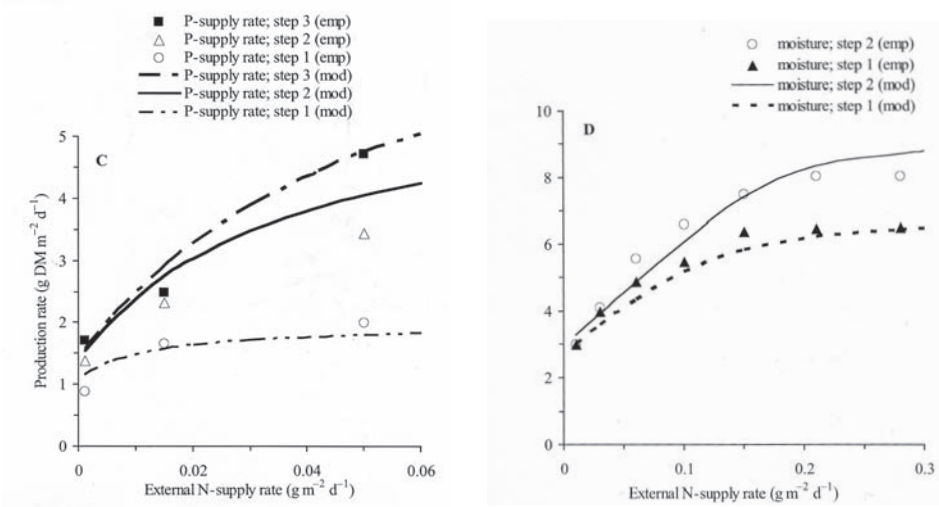

Figure 8 (cont'd).

C: Comparison of the complete model (two nutrients, N and P) with empirical data of Penning De Vries *et al.* (1982). Production rate against external nitrogen supply rate for different constant rates of phosphorus supply. Crop is grass. Parameter values: n_{min} = 0.004; n_{max} = 0.024; p_{min} = 0.0005; p_{max} = 0.0030; λ_N = 0.05; λ_P = 0.005; r_{max} = 8; α_N = 30; α_P = 400; α_{NP} = 600; $S_{N\text{-}ext}$ = 0.01; $S_{P\text{-}ext}$ = 0.001; S_N steps = 0 / 0.015 / 0.05; S_P steps = 0 / 0.005 / 0.015. Assumption: the growing season for grass is 200 days; so 1 g m^{-2} d^{-1} = 2 tons ha^{-1} $year^{-1}$.

D: Comparison of the complete model (nutrient N and 2 moisture levels) with empirical data of Van Heemst *et al.* (1978). Production rate against external nitrogen supply rate for different constant levels of soil moisture. Crop is grass. Parameter values: n_{min} = 0.03; n_{max} = 0.03; $h2o_{min}$ = 0.17; $h2o_{max}$ = 0.19; λ_N = 0.90; λ_{H2O} = 0.009; r_{max} = 10; α_N = 999999; α_{H2O} = 0.0008; $\alpha_{N\text{-}H2O}$ = 0.02; $S_{N\text{-}ext}$ = 0.09; $S_{H2O\text{-}ext}$ = 0; S_N steps = 0.01 / 0.03 / 0.06 / 0.10 / 0.15 / 0.21 / 0.28; S_{H2O} steps = 250 / 1000. Assuming a product with a water content varying between 0.17 and 0.19 (let us say hay with 18% DM). The model permits to regard water as a 'nutrient'. In our concept water only differs from nutrients in parameter values, which have another order of magnitude. Assuming a growing season of 200 days, 1 g m^{-2} d^{-1} equals 2 tons ha^{-1} $year^{-1}$.

manuscript, and (3) that of the complete M–M model with a multiplicative term.

The feature of shift between ideal-types of the 'integrated model' is explained by describing an important extension of the 'basic production function' – that of distinction between the concepts soil *nutrient stock* and *nutrient supply rate*. The soil nutrient stock connects three processes of the model, *nutrient supply*, *nutrient loss* and *nutrient uptake*, in a dynamic equilibrium (Equation 26).

If we plot the production rate as a function of the nitrogen supply rate while keeping the phosphorus supply rate (and other production factors) constant, depending on the parameter values α_{NP}, α_N and λ_N, the following variants emerge:

1. The 'Full model variant', which is obtained for a 'basic production function' with main terms as well as an interaction term. Conditions: α_{NP} equals exactly $\alpha_N \times \alpha_P / r_{max}$ for this variant.

2. The 'Greenwood variant', which results if α_{NP} is large, α_N is small (and/or λ_N is large), and r_{max} is sufficiently large.
3. The 'De Wit variant', which is obtained if α_{NP} is small compared with α_N, and/or λ_N is large, and r_{max} is sufficiently large.
4. The variants 1, 2 and 3, all of which are saturation curves, shift towards the 'Liebig variant' under the following conditions: (i) an extremely large value of α_N and a moderately large value of α_{NP} (and/or the relative loss rate, λ_N, is small), and (ii) an extremely large value of α_{NP} and a moderately large value of α_N (and/or the relative loss rate, λ_N, is small).
5. The 'Liebscher variant', which is obtained for parameter values somewhere in between those of the 'Greenwood variant', the 'De Wit variant' and the 'Liebig variant'. For a high ratio α_N / λ_N the 'Liebscher variant' also shifts into the direction of the 'Liebig variant'.

Most functions mentioned in this paper have 'decreasing marginal returns' ('Greenwood') or constant (followed by 0) marginal returns ('Liebig'). Only variants with a substantial influence of the multiplicative interaction term have the potential of giving 'increasing marginal returns'. This feature can be obtained in the multiplicative variant of the M–M model by raising the supply of multiple nutrients in required proportions – instead of raising the supply of a single nutrient only and keeping the other ones constant.

Several conditions may reduce the manifestation of 'increasing marginal returns': this can hardly be realized by the 'integrated model' presented in the foregoing, mainly because of the linearizing effect of the uptake resistance in the soil. Even with multiplicative effects at the root level, the Liebig behaviour arises at the supply level. The process is further reinforced by some other conditions. 'Increasing marginal returns' can hardly be expected in situations of highly productive systems in which the production rates are close to the asymptotic maximum of the supply rate. Let us summarize the conditions that preclude or weaken the manifestation of 'increasing marginal returns': (1) high supply rates, (2) large soil nutrient stocks, (3) large affinity parameters for the nutrients, (3) low relative loss rates of the nutrients, (4) a low maximum production rate, (5) spatial and/or temporal variability of the soil, and (6) imperfect proportionality of nutrient availability.

In practice, 'increasing marginal returns' can be expected mainly in two situations. The first situation is that of nutrient-poor sandy soils where leaching losses are large. If in that situation the plants respond to both nitrogen and phosphorus by root expansion, some super-proportional effect can be found at low supply rates. Because of the presence of the multiplicative interaction term, such a situation is within the scope of our model. But – as explained in the foregoing – this effect is not likely to occur under conditions of large nutrient supplies as used in high productive agriculture.

The second situation arises when passing a nutrient availability threshold. For example, if phosphate is applied in a very phosphorus-poor situation, first a threshold level has to be satisfied before any response on production is found. This is due to chemical fixation, rendering the phosphorus unavailable to the plant. Not until this demand has been satisfied, phosphorus will be available to the plant. This is a situation that is actually beyond the concepts of our model.

From a comparison of our model with empirical data it appeared that a simplified variant of the 'integrated model' with the main terms only, i.e., a variant without 'increasing marginal returns' (the 'Greenwood variant'), sufficed to describe a number of empirical production curves found in the literature (Greenwood *et al.*, 1971; Van Heemst *et al.*1978; Penning De Vries & Djiteye, 1982).

With the relatively large nutrient supply rates used in the Netherlands and the rest of Western Europe, 'increasing marginal returns' for nutrients can hardly be expected, not even in the case of exactly proportional supply rates – no matter what form the 'basic production function' has.

Further research may include a sensitivity analysis of the model, empirical validation with other datasets, and the addition of nutrient input prices, product prices and nutrient loss abatement prices to support input optimization studies.

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