USING THE EXPOLINEAR GROWTH EQUATION TO ANALYSE RESOURCE CAPTURE

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Introduction

Complex growth models have the potential to synthesize knowledge from different disciplinary fields, and to evaluate their combined behaviour. This process of putting models together, running them and studying their output, comprises the activity of 'simulation' (Rabbinge and De Wit, 1989), and will enhance our understanding if we do it with an open mind and a some sensible amount of self-criticism. Even in relatively simple models the complexity of interactions is baffling. Yet sometimes it is possible to discern guiding principles in the behaviour of the models. Being a simplified representation of reality, models should reflect nature also in this respect. Both careful real world experimentation and model analysis will be needed to find such guiding principles.

This quest for guiding principles is essential in science. Models can serve a useful role in assisting the scientist in this task, but in addition to the 'simulation' approach in the traditional sense, there is also a line of model research which explores highly simplified models (Monteith, 1981a; Waggoner, 1990). These models will perhaps suffer from lack of realism, but they do have the advantage of highlighting those features of dominating processes that we want to emphasize. In this respect these models are more subjective than large, comprehensive models.

Whereas the individual scientist may prefer one type of modelling or the other, it appears to the author that in general the use of complex models and of simplified models should go hand in hand (Spitters, 1990).

A simplified model will be used in this chapter to aid our understanding of a few features of crop growth and resource capture, rather than for a well-validated and generalized description of many of its aspects.

The expolinear growth equation will be used to investigate the phenomenon of apparent down-regulation of relative growth rate under increased CO_2, and the theory will be extended to allow for constrained leaf area growth, such as occurs under shortage of nitrogen.

A simple growth model: the expolinear growth equation

The basis of the analysis here is the assumption that plant growth follows the expolinear growth curve (Goudriaan and Monteith, 1990). The expolinear

equation provides a continuous transition from the exponential growth phase, observed in young relatively widely spaced plants, to the linear growth phase that is seen later when the leaves have filled the space between plants. At that stage the plants have become so large that they fully compete with each other, so that their combined growth rate will be constrained, and approaches a maximum value. The equation for the expolinear growth curve is:

$$w = \frac{c_m}{r_m} \ln \left\{ 1 + \exp\left(r_m \left(t - t_b\right)\right) \right\} \qquad \left[\text{g m}^{-2}\right] \qquad (1)$$

where:

w is the crop biomass at time t [g m^{-2}]
c_m is the maximum absolute growth rate in the linear phase [g m^{-2} d^{-1}]
r_m is the maximum relative growth rate in the exponential phase [d^{-1}]
t_b is a timing parameter [d]

These three parameters completely describe the growth curve. The initial biomass (w_0) at time zero can be expressed by these three parameters by setting $t = 0$ in the equation, but it is often a more natural sequence to express the timing parameter t_b using initial biomass, i.e.:

$$t_b = -\frac{\ln \left\{ \exp\left(\frac{r_m \, w_0}{c_m}\right) - 1 \right\}}{r_m} \qquad [\text{d}] \qquad (2)$$

This may be useful when we compare treatments that start at the same initial biomass.

The expolinear growth equation is consistent with a few simple and plausible assumptions:

1. Exponential extinction of radiation with leaf area index L, and a constant extinction coefficient k, according to the well-known expression:

$$f = 1 - \exp(-kL) \qquad [\text{-}] \qquad (3)$$

2. A direct proportionality between this fraction f and actual growth rate, c ($c = \mathrm{d}w/\mathrm{d}t$), of biomass:

$$c = c_m f \qquad [\text{g m}^{-2} \text{ d}^{-1}] \qquad (4)$$

3. A constant ratio between leaf area and plant dry matter, leaf area ratio (LAR), that is further separated into leaf weight ratio (LWR) (partitioning to leaves) p_l [-] and specific leaf area (SLA) s [m^2 g^{-1}]:

$$\mathrm{d}L/\mathrm{d}t = p_l s c \qquad [\text{d}^{-1}] \qquad (5)$$

This is the weakest assumption. Later we shall develop an equation for a situation in which partitioning to the leaves decreases after a while.

The potential relative growth rate (RGR) r_m for the early exponential phase can now be expressed as:

$$r_m = k \, p_l \, s \, c_m \quad [\text{d}^{-1}] \qquad (6)$$

Typical parameter values used in this paper are given in *Table 6.1*.

Table 6.1 PARAMETER SET USED FOR CONTROL CALCULATIONS WITH THE EXPOLINEAR EQUATION

Description	Symbol	Value	Unit
Maximum absolute growth of crop biomass	c_m	20	$[\text{g m}^{-2}]$
Partitioning to leaf dry weight	p_l	0.5	[-]
Specific leaf area	s	0.02	$[\text{m}^2 \text{ g}^{-1}]$
Initial crop biomass	w_0	1	$[\text{g m}^{-2}]$
Extinction coefficient	k	0.7	[-]
Derived variables:			
Maximum (potential) relative growth rate	r_m	0.14	$[\text{d}^{-1}]$
Timing parameter ('lost time')	t_b	35.4	[d]

Down-regulation of RGR, a functional adaptation?

Plant growth experiments with increased CO_2 have shown that biomass increased by 30–40% upon CO_2 doubling, at least when the plants were grown under non-limiting nutrients (Kimball, 1983). This increase is usually attributed to enhanced photosynthesis (Lawlor and Mitchell, 1991), although decreased respiration may also be a contributing factor (Amthor, 1991). The method of growth analysis can be used to discern between functional and morphological factors that give rise to growth stimulation. The classical growth analysis, developed for young plants, emphasizes *relative growth rate* and separates it into *growth per leaf area* (the functional component net assimilation rate ('NAR') or unit leaf rate ('ULR')) and in *leaf area per unit of biomass* (the morphological component 'LAR'). In a comparison of relative growth rate in Equation 6 with the familiar expression from classical growth analysis RGR=NAR*LWR*SLA, the term 'NAR' becomes equal to $k \, c_m$ in the unshaded exponential phase.

The difference between fast and slow growing species is mainly caused by a difference in morphology (LWR and SLA) (Poorter, 1993), but the effect of increased CO_2 is caused by an increased rate of growth per unit leaf area ('NAR'). Increased CO_2 may alter morphology as well, but if it does it will suppress rather than enhance the effect of increased growth rate per unit leaf area. This morphological adaptation to higher CO_2 consists of increased thickening of leaves, so that more biomass is needed to produce the same leaf area (Lemon, 1983).

When the time courses of relative growth rate of control plants and of plants grown under higher CO_2 are plotted together *versus* time, it seems that the initial stimulus of RGR disappears quickly, and may even turn into a reduction

(Poorter, 1993). The question now is, whether this experimental finding is largely a result of functional down-regulation, such as a reduction in photosynthetic capacity (Besford and Hand, 1989; Besford, Ludwig and Withers, 1990; Bowes, 1991), or whether there is a simple mechanistic explanation.

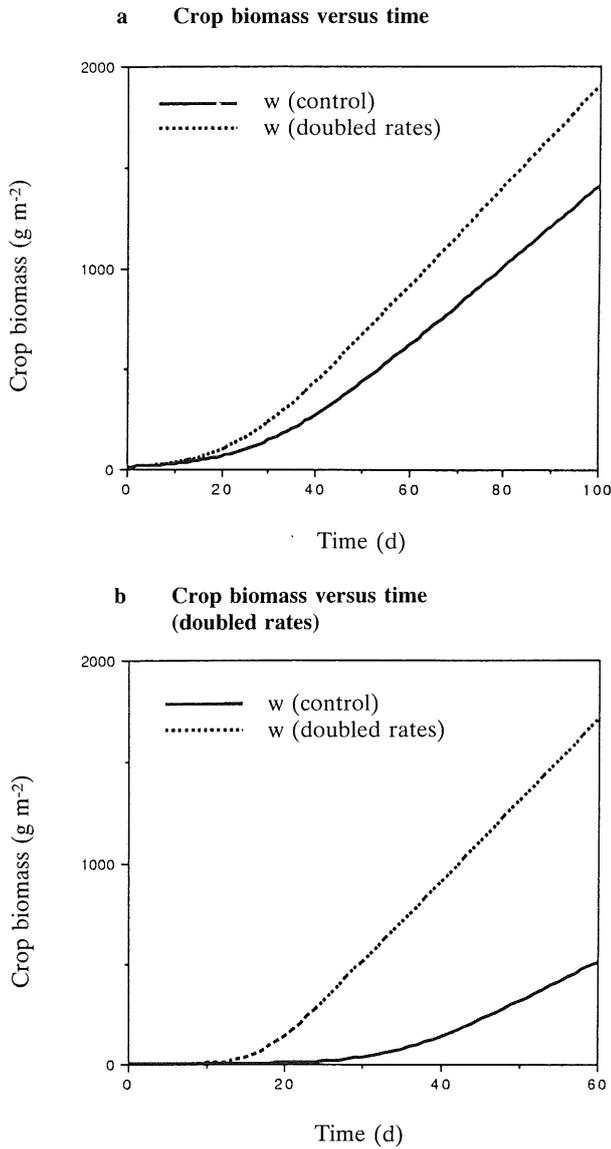The methodology chosen here is to investigate what happens with RGR

a   Crop biomass versus time

b   Crop biomass versus time (doubled rates)

Figure 6.1   Calculated crop biomass according to the expolinear equation. The higher curve was calculated for increased growth parameters c_m and r_m. (**a**) Growth parameters differed by a factor 1.3 (**b**) Growth parameters differed by a factor 2

according to the expolinear equation, if we assume that there is *no down-regulation at all* in any functional or morphological parameter that describes plant growth. First of all, let us assume that the CO_2 effect is expressed by an increased maximum linear growth rate c_m. Let us also assume that there is no morphological adaptation, i.e., that the partitioning coefficient p_l and leaf area per leaf dry weight s are unchanged. Clearly, this is a simplification of reality, but it helps to discern the effects of increased mutual shading from adaptation in functional and morphological parameters. In this simplified situation the potential relative growth rate r_m according to Equation 6 will be changed in direct proportion to c_m. The ratio $c_m : r_m$ will not be affected, but the timing parameter t_b (Equation 2) in inversely related to r_m.

The behaviour of the expolinear growth equation in these two situations can now be easily evaluated and compared, using altered values for c_m and r_m. When both c_m and r_m are increased by 30%, which is a typical value for the effect of CO_2-enrichment, graphs such as shown in *Figure 6.1a* are obtained for the time courses of dry biomass. The biomasses attained in the end differ by a number that is slightly greater than the stimulus factor 1.3 on growth rate, because the value of t_b ('lost time'; Monteith, 1981b) has also been reduced under these improved growth circumstances.

The time course of relative growth rate shows a peculiar behaviour (*Figure 6.2a*). Its initial value is about a factor 1.3 higher than in the control, but it soon declines to a value quite close to the control, and it even falls below it. This kind of pattern, if observed in experimental data, might be interpreted as down-regulation of the growth processes, attributable to all sorts of internal adaptations that return the photosynthetic rate to the value of the control situation.

In fact, the primary explanation is more mechanistic. In order to highlight this effect, the maximum growth rate c_m and potential relative growth r_m were multiplied by a factor of 2 instead of 1.3, so that the results became more contrasting (*Figure 6.1b, 6.2b*). *Absolute* growth rate was much larger at any time during the growth period, but *relative* growth rate soon declined to a value that was even lower than in the control run. The explanation becomes quite clear, when absolute and relative growth rate are plotted not *versus* time, but *versus* biomass (*Figure 6.3*). In this representation the multiplication factor of 2 is retained. In *Figure 6.3a* absolute growth rate is given every 5 days, showing that the distance between each point in time is much larger in the doubled-rate run, than in the control run. The relationship between absolute growth rate c and biomass w is given by Equations 3 and 4, and by using $L = p_l s w$:

$$c = c_m \{1 - \exp(- k \, p_l \, s \, w)\} \qquad [\text{g m}^{-2}\,\text{d}^{-1}] \qquad (7)$$

The factors $k \, p_l \, s$ are not affected by doubling c_m, and so the graphs differ only by the multiplication factor that operates on c_m, a scaling factor in the vertical direction. The scaling factor in the horizontal direction $(k \, p_l \, s)^{-1}$ remains the same. But, relative growth rate can also be read from this graph. It is the slope of a straight line from the origin to the point of the graph at the moment considered. Initially these slopes differ by a factor of two, but for the doubled-rate situation the curve levels off much sooner, because the scaling biomass $(k \, p_l \, s)^{-1}$ is reached much earlier. In simpler terms, the occurrence of plant shading is so strongly accelerated that the reduction of relative growth rate sets in much earlier. This effect dominates the time course of relative growth rate, even though the absolute
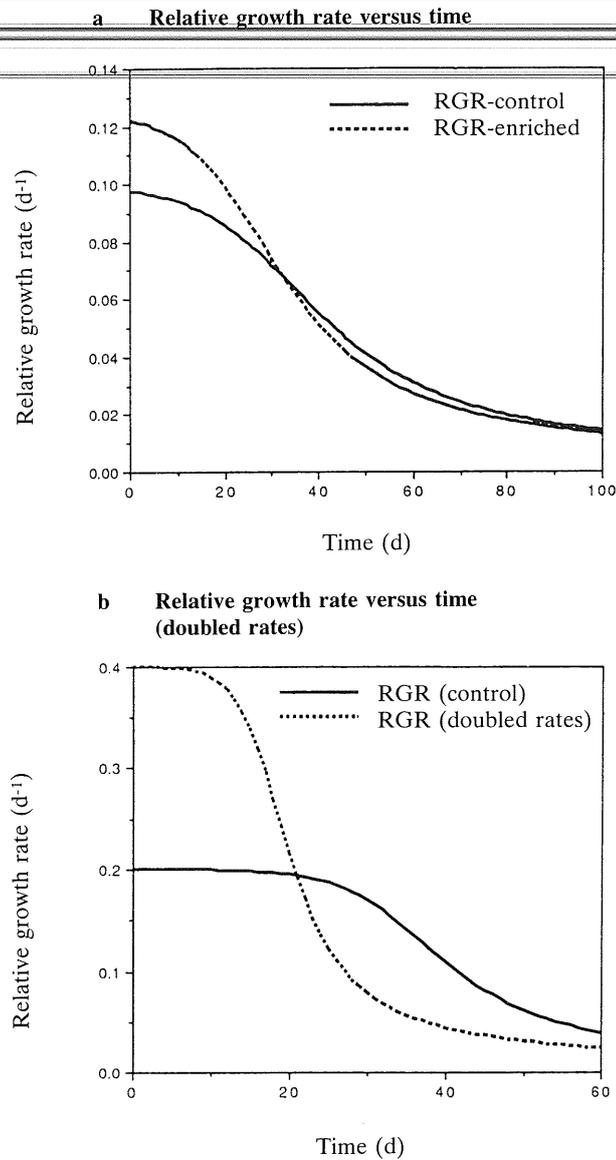
a   Relative growth rate versus time

b   **Relative growth rate versus time**
     (doubled rates)

Time (d)

Figure 6.2   Time courses of actual relative growth rate for the curves as in
Figure 6.1. The initial difference in relative growth rate soon disappears. (a)
Growth parameters differed by a factor 1.3 (b) Growth parameters differed by
a factor 2

growth rate remains much higher at any moment. Biomass can also be written as
initial biomass times $\exp(\int r \, \mathrm{d}t)$.

Therefore, the largest ratio of biomasses occurs when the integrals of $r \, \mathrm{d}t$ differ
most, e.g. at the moment of crossing over of the two lines in *Figure 6.2*, here
at time 21 (*Figure 6.2b*). After that moment, the ratio of the biomasses starts

to decline again. In practice, the graph of RGR versus time does not offer a convenient way to assess the effect on final biomass. A barely visible difference in integrated relative growth rate may have a large effect on final biomass. The time plot of absolute growth rate is a better measure for this purpose. The best method to see if *functional* adaptation occurs, is plotting growth rate *versus* biomass, or leaf area, rather than *versus* time (*Figure 6.3b*).
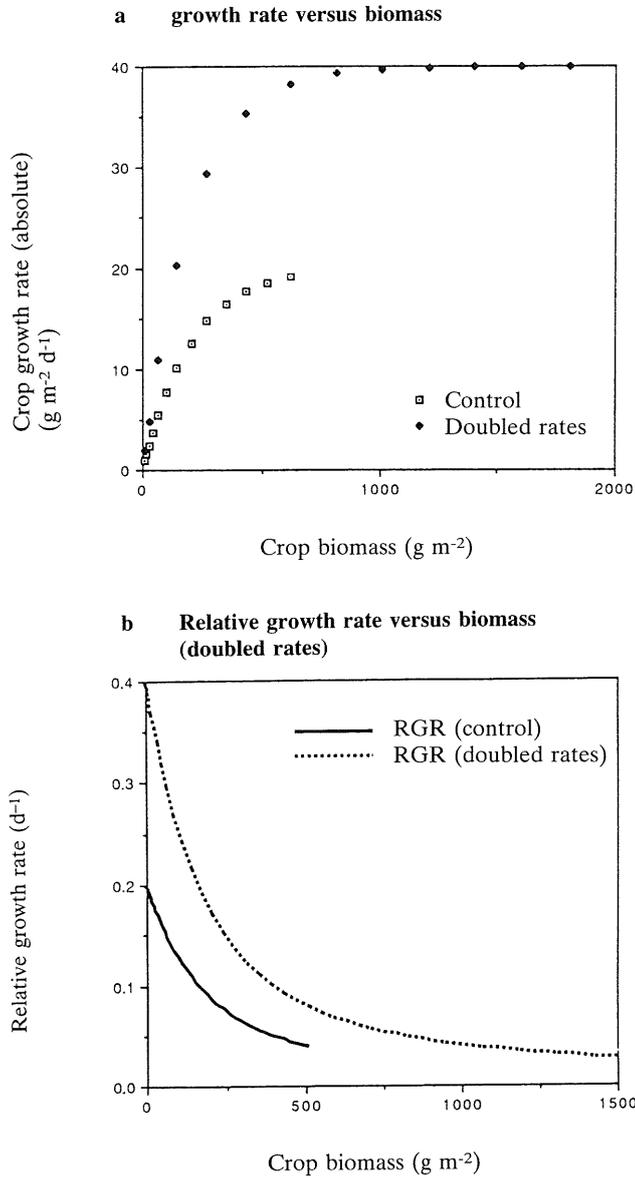
a   growth rate versus biomass

Crop biomass (g m^{-2})

b   Relative growth rate versus biomass
(doubled rates)

Crop biomass (g m^{-2})

Figure 6.3   Absolute growth rate (**a**) and relative growth rate (**b**) as a function of biomass, for the control and doubled parameter situation.

The expolinear equation for nitrogen limited situations

Canopy photosynthesis clearly increases as a function of leaf area index, due to increasing light interception. Equation 4 expresses the relation between crop growth rate c and fraction of intercepted radiation f as a simple linear relation. However, the relation between gross canopy photosynthesis and intercepted fraction is not simply a straight line because lower leaves operate at lower light levels and tend to exhibit a higher light use efficiency (when photosynthetic parameters are uniform). Gross canopy photosynthesis thus increases more rapidly than fraction f of intercepted radiation.

Complications tend to straighten out this upward curved relation. Respiration increases when leaf area index increases, and this will certainly restrict *net* photosynthesis. Because a large portion of respiration is proportional to growth itself, the relative effects on gross and net photosynthesis are less different than one would initially think.

Another important factor is adaptation of leaf photosynthetic capacity to lower light levels deep in the canopy. This adaptation mainly affects maximum photosynthetic capacity ('A_{max}') (DeJong and Doyle, 1985), and is mediated by a lower leaf nitrogen content in the shade. Photosynthetic capacity is strongly related to leaf nitrogen (Van Keulen and Seligman, 1987; Leuning, Cromer and Rance, 1991a), but light use efficiency is not. Therefore the scaling factor for light intensity with respect to photosynthesis declines together with average light level, and mean light use efficiency is rather invariant with canopy depth. This effect tends to linearize the relationship of canopy photosynthesis with fraction of light intercepted (Leuning, Wang and Cromer, 1991b), and indeed even with canopy nitrogen (Field, 1991). For high leaf area indices it also means an improvement of nitrogen use efficiency, as the lower leaves require less nitrogen.

The linear growth phase of the original expolinear equation never ceases. A supposedly constant partitioning of assimilates to new leaf area causes the leaf area index to grow indefinitely as well. This behaviour, although unrealistic, does not always pose a problem. For instance, beyond a leaf area index of 5, the fraction of radiation intercepted is almost unity anyway and it hardly matters to the computed rate of growth whether leaf area index increases any further.

However, for calculation of nitrogen expenditure the situation is different. Green leaf area is particularly costly in terms of nitrogen demand, and when there is a limited amount of nitrogen available, this will pose an upper limit to the formation of leaf area index. A rather crude way to impose this upper limit in a simple model is to truncate any further increase in leaf area index as soon as the upper limit imposed by shortage of nitrogen (or of another requirement such as water) is reached. This method will however cause a discontinuity in the growth rate of leaf area, and also in the calculated uptake rate of nitrogen flowing to the leaves.

A more realistic growth pattern must allow for a gradual reduction in the formation rate of leaf area, while it approaches a maximum possible leaf area. Such a growth curve can be obtained by a modification of the expolinear growth equation. The maximum growth rate c_m is now further constrained by a factor f_m between 0 and 1 and which is independent of t or w:

$$w = \frac{c_m f_m}{r_m} \ln\{1 + \exp(r_m(t - t_b))\} \qquad [\text{g m}^{-2}] \qquad (8)$$

This factor f_m allows for the model assumption that light interception will not exceed a value of $1 - \exp(-k\,L_m)$. The shape of this modified growth curve is still expolinear, but the difference with the original expression is that the linear growth phase proceeds with a reduced, 'apparent', linear growth rate $c_{m,app}$, which is given by the product of the potential growth rate c_m and the maximum interception fraction f_m. This modification has no effect on the early exponential phase, since the maximum relative growth r_m is the same.

Now we should consider what this modification means in terms of the growth pattern of leaf area index. First Equations 3 and 4 are combined to give:

$$\frac{dw}{dt} = c_m\{1 - \exp(-k\,L)\} \qquad [\text{g m}^{-2}\,\text{d}^{-1}] \qquad (9)$$

This expression for dry matter growth rate is equated to the first derivative of the modified expolinear growth equation:

$$\frac{dw}{dt} = c_m\{1 - \exp(-k\,L)\} = \frac{c_m f_m \exp\{r_m(t - t_b)\}}{1 + \exp\{r_m(t - t_b)\}} \qquad (10)$$

This combination can give us leaf area index L as an explicit function of time t and of its maximum value L_m, defined by $f_m = 1 - \exp(-k\,L_m)$:

$$L = \frac{1}{k}\ln\left[\frac{1 + \exp\{r_m(t - t_b)\}}{1 + \exp\{r_m(t - t_b) - k\,L_m\}}\right] \qquad [\text{m}^2\,\text{m}^{-2}] \qquad (11)$$

From this equation we see that $L \to L_m$ when $t \gg t_b$. The equation for the rate of leaf area formation (Equation 5) is now modified to:

$$\frac{dL}{dt} = p_1 s\, c\, \frac{1 - \exp\{-k(L_m - L)\}}{1 - \exp\{-k\,L_m\}} \qquad [\text{m}^2\,\text{m}^{-2}\,\text{d}^{-1}] \qquad (12)$$

This multiplication factor allows for a reduction that increases until the maximum leaf area index L_m is reached.

When this methodology is applied, an S-shaped growth curve of leaf area index appears. It is remarkable that the expolinear equation still stands up in this generalization. By permitting levelling off of leaf area growth a considerable theoretical objection against the expolinear equation is removed.

Nitrogen uptake rate of the foliage can be calculated as the rate of increase of the amount of nitrogen in the foliage. When all leaves have uniform nitrogen content, the uptake rate is simply the derivative of the S-shaped growth curve of leaf area index multiplied by leaf nitrogen content. This growth pattern generates
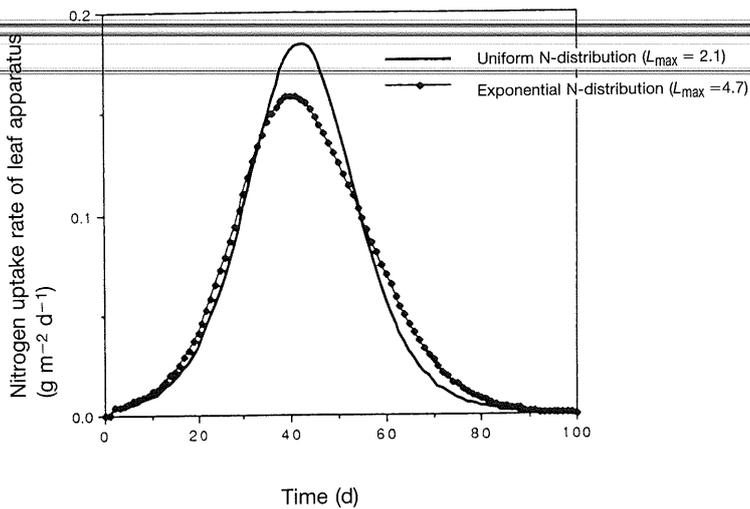
Figure 6.4 Nitrogen uptake rate to sustain leaf area growth. The total amount of nitrogen available for leaf area growth was set at 5.5 g m^{-2} (ground area). For the uniform distribution the maximum LAI was 2.1, but the optimized distribution an LAI of 5 could be formed

a bell shaped curve of nitrogen uptake rate of the green leaf mass (*Figure 6.4*). When leaf nitrogen content declines with canopy depth, the pattern of nitrogen uptake rate is still bell-shaped, but with an earlier and lower peak. In both nitrogen distribution modes, the bell shape applies qualitatively.

When there is only a limited amount of nitrogen available, this limitation will constrain leaf area growth, usually forcing it to a growth curve very much like the bell-shape presented before. For a given amount of nitrogen as a constraint, we can conversely infer the leaf area growth pattern that is possible on basis of this limited amount. As a typical situation, total amount of nitrogen available for uptake by the leaves was set at 5.5 g m^{-2} of ground area. When all leaves have a uniform nitrogen content of 2.6 g m^{-2} of leaf area, a total leaf area index can be formed of 2.1 , resulting in a maximum fraction of intercepted radiation of about 0.77. At the peak of leaf area formation, the nitrogen uptake rate reached about 0.18 gN m^{-2} d^{-1} and the mean duration of the uptake period was about 30 days.

The next step was to model the situation in which the nitrogen content was adapted to the light profile (Werger and Hirose, 1991). Only the topmost leaves have then the same content as in the first case, and deeper down in the canopy the leaf nitrogen content declines in such a way that the A_{max} profile follows the light profile. As a result a larger leaf area index could be formed (4.7 instead of 2.1), more light could be intercepted, and a higher assimilation rate per unit ground area could be maintained. Using Equation 12, by day 100 the N-optimized canopy had formed a biomass of 1250 g m^{-2}, whereas the N-uniform canopy had only formed 1000 g m^{-2}. This example shows the potential benefit of optimizing the distribution of nitrogen over the leaf canopy. For a given amount of available nitrogen, the difference between the two ways of distributing the amount of

nitrogen over the leaves is only slight in terms of the time course of nitrogen uptake rate (*Figure 6.4*).

Discussion

In this paper no comparison with actual experimental data has been given. The ideas and graphs are generalizations based on literature data that provided the background information. The phenomena described in this paper can certainly be modelled by more complex, comprehensive models, and indeed they should be. Concentrating on one simple model structure, this paper intends to highlight a few interesting processes, which are perhaps less clearly seen when a more complex model is used. Monteith (1990) has recognized the importance of simple models throughout his work, and this paper was written in this tradition. In the real world, the complexity of processes may blur the clean effects suggested here, but not totally. The author preferred to concentrate on a few main lines of thought, rather than to get lost in a synthesizing complex model. Yet complex models are needed to bring together the many effects that simultaneously occur in the real world. It would be a mistake to abandon complex growth models for fear of chaos. The most fruitful way is to explore both methodologies and to see how they can be used to complement each other.

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