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## Optimization of nitrogen distribution and of leaf area index for maximum canopy assimilation rate

J. Goudriaan

Department of Theoretical Production Ecology, Agricultural University, P.O.Box 430,  
6700 AA Wageningen, The Netherlands.

### I. Optimum nitrogen allocation to leaves follows the light profile

#### Introduction

This part I of the paper deals with the question how a given quantity of nitrogen should be distributed over the leaf canopy to reach maximum canopy photosynthesis. Maximization of canopy assimilation may be viewed as a goal that is anthropocentric, irrelevant to plants. Yet, the evidence is that implementation of this goal leads to a nitrogen distribution similar to the one observed in the field. Many studies (see review in Van Keulen & Seligman, 1987) have shown strong positive correlations between photosynthetic capacity of leaves and their nitrogen content. In addition, these two characteristics are found to be correlated with the mean light exposure of leaves (Acock et al., 1978; DeJong & Doyle, 1985). Hirose & Werger (1987) investigated the optimum distribution of nitrogen over the leaf canopy, by optimizing its daily net CO<sub>2</sub> assimilation using a simulation method. Inserting measured relationships between nitrogen content and photosynthetic properties into a model for canopy photosynthesis, they found that most nitrogen should be allocated to the leaves that are located in the higher canopy levels, where they are exposed to higher radiation intensities.

The mathematical analysis presented in this paper shows that optimization of canopy photosynthesis leads to a distribution of nitrogen over the leaf canopy in such a way that photosynthetic capacity of leaves is proportional to the mean absorbed photosynthetically active radiation.

#### Description of leaf assimilation rate

At low irradiance gross CO<sub>2</sub> assimilation  $A$  ( $\mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) of leaves increases linearly with absorbed PAR  $H$  ( $\text{W m}^{-2}$ ):

$$A = \epsilon H \quad (1)$$

where  $\varepsilon$  is quantum efficiency in  $\mu\text{g CO}_2 \text{ J}^{-1}$  (PAR).

For high irradiances the relationship between  $A$  and  $H$  levels off and approaches an asymptotic maximum  $A_m$ . The general expression for this type of relationship is:

$$A = A_m f(A_m, \varepsilon H) \quad (2)$$

where gross leaf assimilation is the product of maximum assimilation rate  $A_m$  (sometimes called photosynthetic capacity) and a dimensionless saturation function  $f$  which rises from 0 to 1 with increasing absorbed PAR. In almost all empirical expressions,  $A_m$  and  $\varepsilon H$  occur together in the dimensionless combination  $\varepsilon H/A_m$ , for example:

$$A = A_m \min(1, \varepsilon H/A_m) \quad (3a)$$

$$A = A_m (1 - \exp(-\varepsilon H/A_m)) \quad (3b)$$

$$A = A_m (\varepsilon H/A_m) / (1 + \varepsilon H/A_m) \quad (3c)$$

$$A = A_m (1 + \varepsilon H/A_m - \{ (1 + \varepsilon H/A_m)^2 - 4\theta \varepsilon H/A_m \}^{0.5}) / (2\theta) \quad (3d)$$

which represents the Blackman response, the negative exponential, the hyperbola and the nonrectangular hyperbola, respectively. The latter function contains an additional parameter  $\theta$  defining the shape of the function (Marshall & Biscoe, 1980).

These expressions for  $A$  can be generalised into:

$$A = A_m f(\varepsilon H/A_m, \text{and other parameters}) \quad (4)$$

The parameters  $A_m$ ,  $\varepsilon$  and  $\theta$  may vary simultaneously with nitrogen content  $N$  ( $\text{g m}^{-2}$ ) of the leaf tissue. Note that  $f$  varies between 0 and 1.

### Optimization of nitrogen distribution

Optimum distribution requires constant marginal returns of nitrogen with respect to leaf photosynthesis over the entire canopy. The rationale for this statement is simple: as long as the benefit of a small increase in nitrogen content is not the same for every leaf position in the canopy, the crop has not reached an optimum distribution yet, since improvement would still be possible by redistribution.

Translating this condition into mathematical terms implies that the derivative of  $A$  with respect to leaf nitrogen content  $N$  should be independent of leaf location. The effect of nitrogen content on dark respiration is neglected here, i.e. it is assumed that the optimization for net and gross assimilation rate is the same.

The first derivative of  $A$  with respect to  $N$  is given by:

$$dA/dN = d(A_m f \varepsilon H/A_m) / dN \quad (5)$$

For brevity of notation the 'other parameters' of Eq. 4 are omitted.

In this analysis it is assumed that nitrogen content only influences  $A_m$ . Optimization through other photosynthetic parameters such as  $\epsilon$ ,  $\theta$  or dark respiration rate is not investigated since experimental evidence such as presented by DeJong & Doyle (1985) and by Hirose & Werger (1987) shows that they are much less dependent on nitrogen content.

The dependence of  $A_m$  on leaf nitrogen can be presented schematically by a linear relationship (Figure 1) where characteristics are used that are typical for  $C_3$ -species (Table 1).

Table 1. Parameter values used, typical for  $C_3$ -species. (Van Keulen & Seligman, 1987; Penning de Vries & Van Laar, 1982).

Threshold of nitrogen content for photosynthesis	$N_b$	$0.3 \text{ g m}^{-2}$
Photosynthetic nitrogen use efficiency	$\alpha$	$1000 \mu\text{g CO}_2 \text{ m}^{-2} \text{ s}^{-1} \text{ g(N)}^{-1}$
Photosynthetic light use efficiency	$\epsilon$	$11 \mu\text{g CO}_2 \text{ J}^{-1}$
Extinction coefficient	$K$	0.7

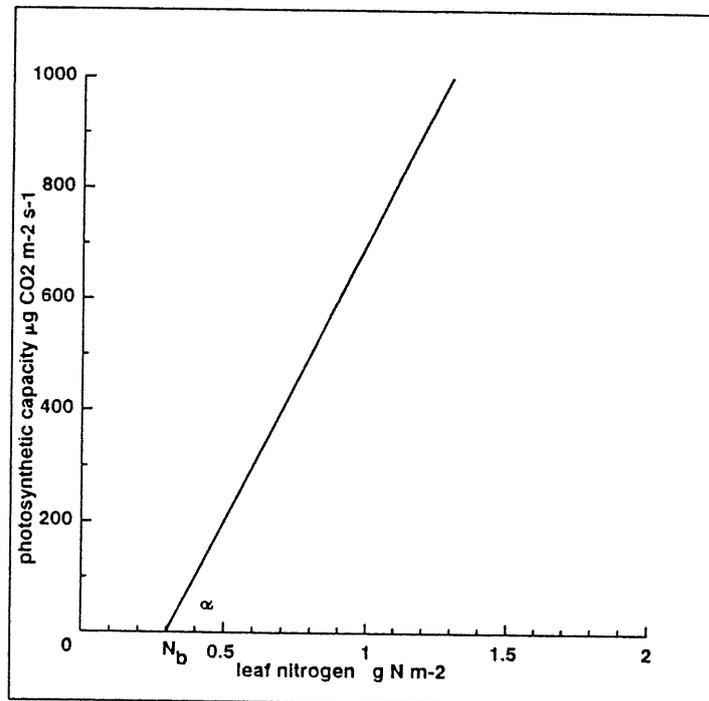


Figure 1. Maximum  $\text{CO}_2$  assimilation rate per leaf area as a function of leaf nitrogen density. The typical level for the threshold  $N_b$  was  $0.3 \text{ g m}^{-2}$  and the slope  $\alpha$  was about  $1 \text{ mg of CO}_2 \text{ s}^{-1} \text{ g}^{-1}$  of N.

The first derivative  $dA/dN$  can be written as:

$$dA/dN = f(\varepsilon H/A_m) dA_m/dN - A_m f'(\varepsilon H/A_m) \varepsilon H/A_m^2 dA_m/dN \quad (6)$$

or

$$dA/dN = \{f(\varepsilon H/A_m) - f'(\varepsilon H/A_m) \varepsilon H/A_m\} dA_m/dN \quad (7)$$

Substituting  $\xi$  for the dimensionless group  $\varepsilon H/A_m$  we find:

$$dA/dN = \{f(\xi) - \xi f'(\xi)\} dA_m/dN \quad (8)$$

It is convenient to write the group  $\{f(\xi) - \xi f'(\xi)\}$ , which is exclusively a function of  $\xi$ , as  $g(\xi)$ . Since  $A_m$  is assumed to be a linear function of  $N$ , the requirement that  $dA/dN$  must be the same for all leaves means that  $g(\xi)$  must be identical for all leaves. This condition is always fulfilled if  $g(\xi)$  is not really a function of  $\xi$ , but a constant. The problem can then be reduced to the differential equation  $f(\xi) - \xi f'(\xi) = c$ , which can be solved and results in  $A = \varepsilon H$ . In this rather trivial situation  $A_m$  is so large that it has lost its effect on the actual assimilation rate. The other, more interesting situation is where the argument  $\xi$  is a constant. In other words, the dimensionless group  $\varepsilon H/A_m$  should be the same for all leaves. Since  $\varepsilon$  was assumed to be constant, this requirement means that  $A_m$  should be proportional to absorbed radiation  $H$ . The conclusion is that the shape of the profile of  $A_m$  must be similar to the shape of the profile of  $H$ . As a first approximation, this shape is independent of light level, so that the shape of the optimum profile of  $A_m$  hardly varies during the day. If this optimum profile is reached,  $A_m$  can be expected to show an exponential decline with depth in the canopy, just as radiation does. The value of  $A_m$  at level  $L$  can be described by:

$$A_m = A_{m,0} \exp(-KL) \quad (9)$$

where  $K$  is the extinction coefficient for PAR, and  $A_{m,0}$  the maximum leaf assimilation rate at the top of the canopy.  $L$  indicates canopy depth in terms over leaf area index above the considered level, and ranges between 0 and  $LAI$ .

According to Eq. 4, the assimilation rate of leaves can be written as

$$A = A_m f(\xi)$$

where  $\xi$  is now constant over canopy depth. Consequently, integration of  $A$  to find canopy assimilation rate is extremely simple and yields, using Eq. 9:

$$A_{tot} = f(\xi) A_{m,0} (1 - \exp(-KLAI)) / K \quad (10)$$

The value of  $f(x)$  can be calculated by substitution of the dimensionless ratio  $\varepsilon KI_0/A_{m,0}$  into one of the response curves of Eq. 3.  $H$  at the top is equal to extinction coefficient  $K$  times incoming radiation  $I_0$ .

A conclusion that follows from the analysis given is that the "extinction" of  $A_m$  should be comparable to that of  $H$ . Indeed, Hirose and Werger (1987) found that the difference in nitrogen content between leaves in the top and in the bottom of the canopy increases with increasing  $LAI$ .

### **Benefit of optimization**

The method presented so far is a qualitative one and does not derive the penalty for deviating from the optimum situation. Therefore a numerical model was used which compares canopy photosynthesis resulting from the optimized profile of  $A_m$  with the one from a uniform profile of  $A_m$ . The conditions chosen were a low flux density of PAR ( $100 \text{ W m}^{-2}$  incoming), and an  $A_m$  (uniform) at 100, 200, 400 and  $1000 \mu\text{g m}^{-2} \text{ s}^{-1}$  respectively. The optimized profile was constructed with the constraint of equal total  $A_m$  (i.e. equal total nitrogen) over the leaf canopy, so that the two profiles cross over. The photosynthesis-light response curve used was the negative exponential one. The results (Figure 2) indicate that any benefit of optimization begins to occur only above  $LAI = 2$ . For lower values of  $LAI$  the range of light intensities is too small for any appreciable benefit of translocating nitrogen from below to above. For the highest value of  $A_m$  chosen ( $1000 \mu\text{g m}^{-2} \text{ s}^{-1}$ ) the benefit is less again than for lower values. For this high value of  $A_m$  even the top leaves are far from light saturation, and translocation from below to above helps little. The conclusion is that optimization is only of appreciable benefit for high values of  $LAI$ , in combination with noticeable light saturation in the top of the canopy.

### **Discussion**

In hedgerow type canopies the radiation profile is not exponential, and the distribution of radiation tends to vary strongly with the position of the sun. Still, in such conditions the nitrogen distribution is expected to correspond to the distribution of mean irradiation. DeJong & Doyle's (1985) observation that  $A_m$  is well correlated with the number of hours that  $H$  exceeds some arbitrary threshold level is in agreement with this line of thought.

The derivation in the analysis presented here does not depend on the precise shape of the photosynthesis-light response curve. Whether it is described by a rectangular hyperbola or some other equation of the type of Eq. 4, the main conclusion is the same. However, if other photosynthetic parameters such as  $\theta$  and  $\varepsilon$  are also a function of the nitrogen content, the analysis will be much more complicated, and the conclusion may be slightly modified. This analysis did not include respiratory costs of the redistribution process itself.

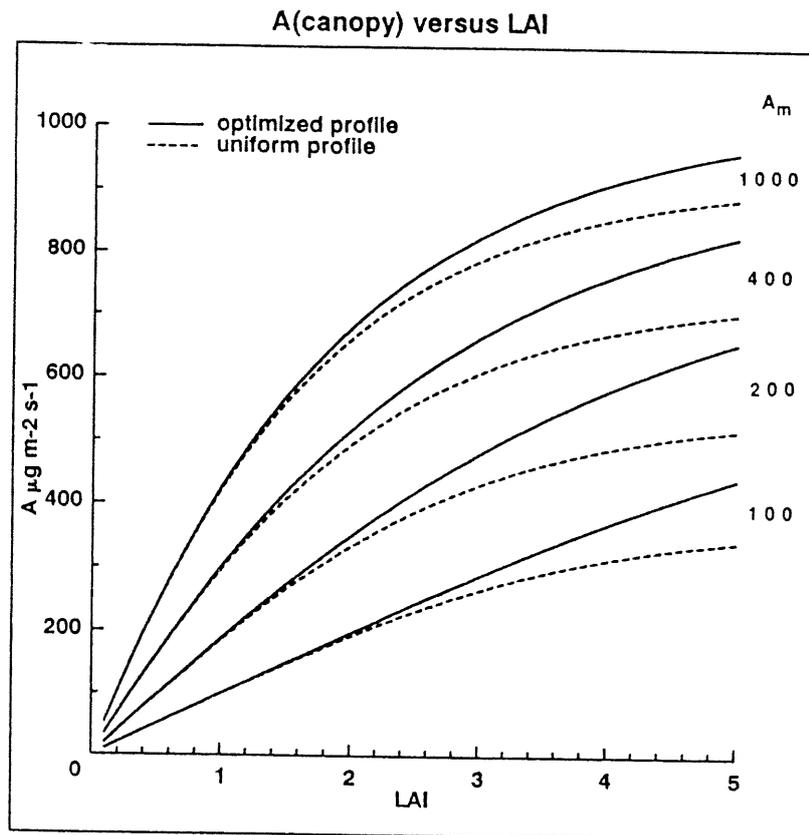


Figure 2.  $\text{CO}_2$  assimilation rate of the leaf canopy for an optimized and for a uniform profile of  $A_m$ . The photosynthesis-light response curve was the negative exponential one. Parameter values were as those given in Table 1.  $A_m$  (uniform) was chosen at 100, 200, 400 and 1000  $\mu\text{g of CO}_2 \text{ m}^{-2} \text{ s}^{-1}$  respectively, and  $A_m$  (optimized) calculated so that the same levels of total  $A_m$  integrated over the leaf canopy was obtained.

These costs will cause a delay in the realization of the real optimum profile and make it more uniform than the theoretical one derived here, especially in a fast growing crop (Field, 1983). Also, the response of photosynthesis to nitrogen may level off at higher nitrogen concentrations, so that the benefit of high nitrogen concentrations in top leaves may be reduced.

There is no question that in leaf canopies the expected relation of leaf nitrogen content with mean irradiation does exist. The mechanism to achieve such a correlation may be based on feedback as well as on feedforward processes. If governed by feedback processes, the leaves that are more illuminated are stronger sinks for nitrogen than the more shaded leaves, which may then even export their nitrogen. A simple feedforward

process on the other hand is just an ontogenetic decrease of nitrogen content with leaf age. Older leaves automatically tend to be more shaded, so that the optimum distribution is automatically approached (Field, 1983). However, in free standing plants the radiation-nitrogen correlation should then no longer exist.

## II. Optimum $LAI$ as a function of incoming radiation and total available nitrogen

### Introduction

As shown in Part I, nitrogen distribution over the leaf canopy can be optimized if the distribution of leaf nitrogen concentration is the same as that for PAR extinction. For high values of  $LAI$  ( $> 2$ ) considerable increases in canopy assimilation rate can be reached. Further optimization for a given quantity of leaf nitrogen  $N$ , available per unit ground area is possible by changing the value of  $LAI$  itself as well.

If in an extremely nitrogen-poor situation all leaves are depleted to the minimum level  $N_b$ , their rate of assimilation will drop to zero. Then at least some canopy photosynthesis could be achieved, just by reducing  $LAI$  in order to increase the nitrogen content of the remaining leaves above the threshold level  $N_b$ . Somewhere in the range between  $LAI = 0$  and  $LAI = N_{tot}/N_b$ , an optimum value of  $LAI$  exists where increase of photosynthetic performance just compensates for reduced light interception. The dependence of canopy photosynthesis on  $LAI$ , given total leaf nitrogen  $N_{tot}$ , is the subject of this part of the paper.

### The nitrogen profile

Since  $A_m$  (Figure 1, Part 1) is given by  $\alpha (N - N_b)$ , the nitrogen profile in the optimized situation follows as

$$N = N_b + A_{m,0} \exp(-KL) / \alpha \quad (11)$$

The total amount of leaf nitrogen per unit ground area is the integral of  $N$  over leaf area, and can be found analytically from integrating Eq. 11 to yield:

$$N_{tot} = N_b LAI + A_{m,0} (1 - \exp(-KLAI)) / (K\alpha) \quad (12)$$

Since  $N_{tot}$  will be considered as a constant, it is more convenient to express  $A_{m,0}$  as a function of  $N_{tot}$ :

$$A_{m,0} = K\alpha (N_{tot} - N_b LAI) / (1 - \exp(-KLAI)) \quad (13)$$

### Canopy photosynthesis

The particular shape of the optimized profile of  $A_m$  provides the possibility of a simple analytical integration of  $A$  over the leaf canopy (Eq. 10, Part 1).

Combination with Eq. 13 gives:

$$A_{\text{tot}} = f(\xi) \alpha (N_{\text{tot}} - N_b LAI) \quad (14)$$

The function  $f(\xi)$  indicates the degree of light saturation of individual leaves (Eq. 3), and has a value between 0 and 1. In the assumed situation of optimized nitrogen distribution it is the same for all leaves, because light and  $A_m$  decrease similarly with canopy depth. Then  $f(\xi)$  can just as well be calculated from the value of  $\xi$  at the top of the canopy:

$$\xi = \varepsilon KI_0 / A_{m,0} \quad (15)$$

substituted into one of the saturation type curves of Eq. 3.

Using Eq. 13 this expression can also be written as

$$\xi = \varepsilon I_0 (1 - \exp(-K LAI)) / (\alpha (N_{\text{tot}} - N_b LAI)) \quad (16)$$

For low values of  $\xi$  the function  $f(\xi)$  approaches  $\xi$  itself. Substitution into Eq. 14 gives

$$A_{\text{tot}} = \varepsilon I_0 (1 - \exp(-K LAI)) \quad \text{for low } \xi \quad (17)$$

This curved relation describes the light limitation of canopy photosynthesis, which is the case for low values of  $LAI$  in combination with a high amount of leaf nitrogen, or for low values of radiation. For high values of  $\xi$  on the other hand, the value of  $f(\xi)$  will tend to unity.  $A_{\text{tot}}$  is then given by

$$A_{\text{tot}} = \alpha (N_{\text{tot}} - N_b LAI) \quad \text{for high } \xi \quad (18)$$

This is a linear relationship with  $LAI$ , but with a negative slope. It describes the region with nitrogen limitation, which occurs for high values of  $LAI$ , in combination with a relatively low amount of leaf nitrogen, or for high radiation levels. Canopy assimilation follows these limits rather precisely if leaf assimilation follows the Blackman type of response curve (Figure 3). Then in the optimized profile all leaves switch simultaneously from light limitation to nitrogen limitation when the optimum value of  $LAI$  is passed. The location of the optimum is then identical to the location of the intersect of the two upper boundaries, and can be calculated by combining Eq. 17 and 18. Unfortunately, this results in an implicit expression for  $LAI$ . However, for low  $LAI$  a reasonable indication of the location of the optimum can be found by combining Eq. 18 with the low  $LAI$  version of Eq. 17,

$A_{\text{tot}} = \epsilon I_0 K LAI$ , which gives:

$$LAI_{\text{opt}} = \alpha N_{\text{tot}} / (\epsilon I_0 K + \alpha N_b) \quad LAI < 1 \quad (19)$$

If the result of Eq. 19 yields a value of  $LAI$  larger than 5, it is better to assume full soil cover and Eq. 17 should be simplified to  $A_{\text{tot}} = \epsilon I_0$ . Combination with Eq. 18 then gives:

$$LAI_{\text{opt}} = (\alpha N_{\text{tot}} - \epsilon I_0) / (\alpha N_b) \quad LAI > 5 \quad (20)$$

Both equations show clearly that the optimum value of  $LAI$  gets larger for increasing total nitrogen  $N_{\text{tot}}$ , for decreasing nitrogen threshold  $N_b$ , and for decreasing radiation  $I_0$ . Because of the implicit occurrence of  $LAI$ , Eq. 19 and 20 are only valid for the extreme ranges of  $LAI$ . For  $N_{\text{tot}}$  however, the combination of Eqs. 17 and 18 returns an explicit solution, which must be interpreted as the level of  $N_{\text{tot}}$  where nitrogen limitation switches to light limitation:

$$N_{\text{tot,switch}} = N_b LAI + \epsilon I_0 (1 - \exp(-K LAI)) / \alpha \quad (21)$$

When a value of 5 is substituted for  $LAI$  into this equation, nitrogen limitation will have disappeared entirely for values of  $N_{\text{tot}}$  larger than  $5.8 \text{ g of N m}^{-2}$ , using the parameter values as given in Table 1, and a radiation level  $I_0$  of  $400 \text{ W(PAR) m}^{-2}$ . If  $LAI$  is only 2, the nitrogen requirement is much less, at  $3.9 \text{ g N m}^{-2}$ .

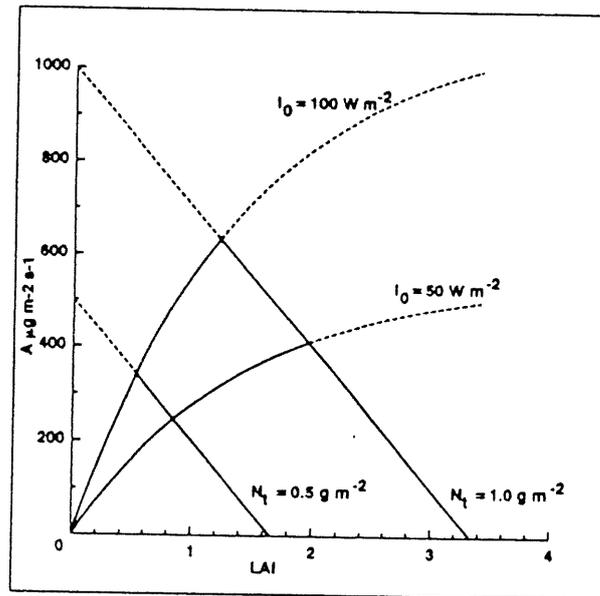


Figure 3. Nitrogen and light limitations to canopy assimilation rate for an optimized nitrogen distribution. Photosynthesis-light response curve was the Blackman response, with parameter values as given in Table 1.

### Benefit of an optimized nitrogen profile

The expressions for  $A_{\text{tot}}$  given above were derived for the optimized profile, which enables simple analytical expressions. In other situations, of which the uniform profile is the simplest one, numerical procedures must replace these expressions. An example of such a numerical evaluation for the dependence of  $A_{\text{tot}}$  on  $LAI$  is shown in Figure 4. In the nitrogen-poor situation the difference between the optimized and the uniform profile is very small. This result is in accordance with part 1, where it was shown that optimization of the profile has hardly an effect below an  $LAI$  of about 2. When there is more nitrogen available, the optimum  $LAI$  shifts upward, both in the optimized and in the uniform profile, but more so in the optimized profile. In other words, non-optimized nitrogen profiles mean a lower value of optimum  $LAI$ , and stronger expression of nitrogen limitation.

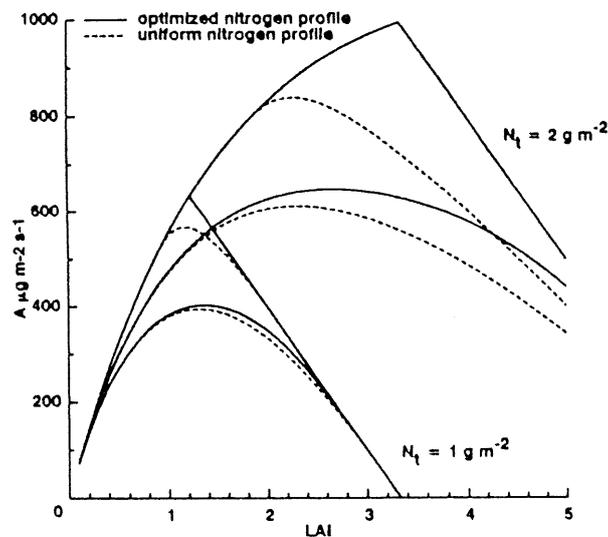


Figure 4. Canopy photosynthesis as a function of  $LAI$  with a fixed amount of total leaf nitrogen  $N_{\text{tot}}$  of 1 and 2  $\text{g m}^{-2}$  (ground area) respectively. The strongly peaked curves result from the Blackman light-response curve of leaf photosynthesis, the more gradual ones from the negative exponential one. Optimized and uniform nitrogen profile had the same amount of total leaf nitrogen and  $I_0$  was  $100 \text{ W m}^{-2}$ . Other parameters were as in Figure 1 and in Figure 3.

### From instantaneous rates to daily total of assimilation

For reasons of simplicity the diurnal course of irradiation was supposed to be sinusoidal over a 12 hour day. This diurnal course was imposed on the model that is formed by the

equations given above, and the instantaneous assimilation rate was integrated to give the diurnal total. The results for the Blackman type response and also for the negative exponential curve are presented in Figures 5a and 5b. The sharp transitions in the Blackman response have been smoothed through the variation of radiation during the day, but the peaks are still more pronounced than for the negative exponential response curve. In both graphs the optimum  $LAI$  clearly decreases with increasing radiation level.

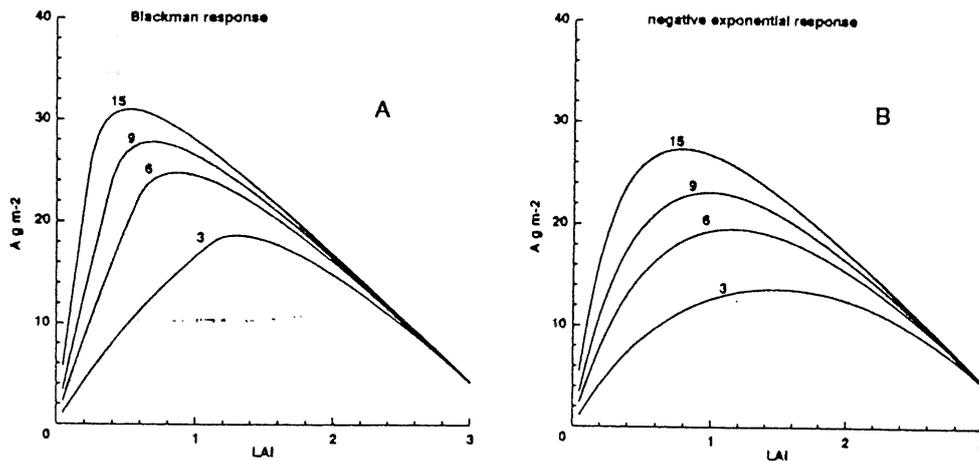


Figure 5. Daily totals of canopy assimilation for four levels of daily total of PAR (3, 6, 9 and 15  $MJ\ m^{-2}$ ). The nitrogen distribution was supposedly optimal. In Figure 5a the curves are shown for the Blackman response and in Figure 5b for the negative exponential relationship.

### Discussion

When the light level increases, the light-limited assimilation is also increased, so that the optimum value of  $LAI$  is decreased (Figure 3). This effect is not important when the available nitrogen is high, since the optimum  $LAI$  is then determined by respiratory costs (not considered here) rather than by nitrogen limitation. However, in nitrogen-poor situations high radiation levels will induce a low value of  $LAI$ , which in practice is hard to distinguish from an effect of water shortage.

The precise shape of the optimum curve of  $A_{tot}$  versus  $LAI$  depends on the photosynthesis-light relationship chosen. The effect of the type of response curve is shown in Figure 6, where the relationship of  $A$  vs.  $LAI$  is given for five irradiation fluxes and for

the Blackman and negative exponential relationship respectively. In case of a Blackman response there are clear-cut boundaries as shown in Figure 3, but for the negative exponential the calculated values of  $A_{tot}$  are always lower.

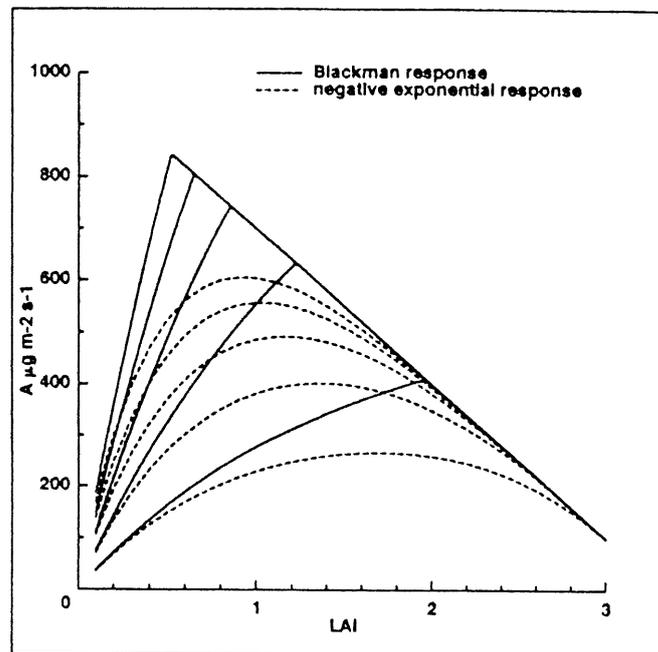


Figure 6. Canopy assimilation rates for five levels of irradiation (50, 100, 150, 200 and 250 J of PAR  $m^{-2} s^{-1}$ ). The other parameters were the same as in Figure 3. The relationships shown were as calculated for a Blackman type response and for a negative exponential relationship. The nitrogen distribution was always supposedly optimal.

The remarkable decrease of optimum  $LAI$  with increasing irradiation is maintained for the negative exponential photosynthesis-light response curve, although the effect is less pronounced than for the Blackman response.

## Summary

Maximum canopy assimilation rate is reached when the nitrogen distribution over the leaf canopy follows the light profile. This conclusion is derived by a mathematical analysis,

using experimental evidence for a linear relation between leaf photosynthetic capacity and its nitrogen content. No assumptions on shape of profile are needed to arrive at this conclusion. The effect of this optimization for canopy photosynthesis becomes only noticeable above a value of *LAI* of 2.

For a given amount of total leaf nitrogen there is an optimum value of *LAI*, determined by light interception on one hand and total leaf nitrogen on the other. Because there is a minimum nitrogen requirement in leaves for photosynthesis, canopy assimilation decreases with increasing *LAI* above this optimum level of *LAI*. This optimum rises with decreasing radiation, increasing total leaf nitrogen, and decreasing minimum nitrogen content in leaves.

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