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Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C₃ and C₄ mono- and dicotyledonous species

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Abstract An analytical model was used to describe the optimal nitrogen distribution. From this model, it was hypothesized that the non-uniformity of the nitrogen distribution increases with the canopy extinction rate for light and the total amount of free nitrogen in the canopy, and that it is independent of the slope of the relation between light saturated photosynthesis (P_m) and leaf nitrogen content (n_L). These hypotheses were tested experimentally for plants with inherently different architectures and different photosynthetic modes. A garden experiment was carried out with a C₃ monocot [rice, *Oryza sativa* (L.)], a C₃ dicot [soybean, *Glycine max* (L.) Merr] a C₄ monocot [sorghum, *Sorghum bicolor* (L.) Moensch] and a C₄ dicot [amarantus, *Amaranthus cruentus* (L.)]. Leaf photosynthetic characteristics as well as light and nitrogen distribution in the canopies of dense stands of these species were measured. The dicot stands were found to have higher extinction coefficients for light than the monocot stands. Dicots also had more non-uniform N distribution patterns. The main difference between the C₃ and C₄ species was that the C₄ species were found to have a greater slope value of the leaf-level $P_m - n_L$ relation. Patterns of N distribution were similar in stands of the C₃ and C₄ species. In general, these experimental results were in accordance with the model predictions, in that the pattern of nitrogen allocation in the canopy is mainly determined by the extinction coefficient for light and the total amount of free nitrogen.

Key words Nitrogen allocation · Optimization
Photosynthesis · Canopy structure
Photosynthetic pathway

Introduction

Net carbon gain of a leaf depends on incident photon flux density (PFD) and nitrogen content per unit area (n_L) (Field and Mooney 1986; Evans 1989). In a vegetation stand both light and nitrogen distribution will therefore affect whole canopy carbon gain.

Patterns of nitrogen distribution and their relation to canopy carbon gain have been extensively studied (Field 1983; Hirose and Werger 1987a, b; Schieving et al. 1992a, b). Hirose and Werger (1987b) formulated a model which describes the optimal pattern of nitrogen distribution for maximal daily canopy photosynthesis. They calculated that canopies with a non-uniform nitrogen distribution having the highest n_L values in the higher, most illuminated regions of the canopy had a photosynthetic advantage over canopies with a uniform distribution of nitrogen where n_L in every leaf equals the mean. It was further found that the pattern of N distribution basically follows the pattern of light distribution in the canopy (Hirose et al. 1989).

A number of leaf and canopy characteristics can be expected to affect patterns of N distribution as well as photosynthetic benefits as a result of N redistribution. Structural characteristics of the canopy such as the leaf area index (F_T) and the extinction coefficient for light (K_L), which determine the distribution of PFD, play an important role (Hirose and Werger 1987a, b). Non-uniformity of N distribution has been shown to increase with increasing stand density and consequent increase in light attenuation in the canopy (Hirose et al. 1988; Schieving et al. 1992a). High nitrogen content of the canopy may enhance non-uniformity of N distribution as more N becomes available for translocation to more illuminated microsites (Hirose and Werger 1987b).

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Finally, patterns of nitrogen distribution and related photosynthetic benefits can be associated with differences in leaf photosynthetic nitrogen use efficiency (PNUE), as the PNUE determines the photosynthetic rate of a leaf with given n_L receiving a given PFD.

Mono- and dicotyledonous growth forms are the two basic architectural modes of canopy organization found in herbaceous plants (Hirose et al. 1989). Monocot species generally have canopies with more vertically inclined leaves than dicot species (Monsi and Saeki 1953). With the vertical component of sky radiation predominating, K_L increases with decreasing leaf inclination. Typical values of K_L are 0.4–0.7 for monocot and 0.65–1.0 for dicot stands (Monsi and Saeki 1953).

Species with the C_4 photosynthetic pathway typically have a higher PNUE than those possessing the C_3 pathway (Brown 1978). This is basically because the C_4 -concentrating mechanism leads to CO_2 saturation of Rubisco (Osmond et al. 1982). Furthermore, C_4 species are generally found to have lower leaf N contents (Brown 1978; Sage and Pearcy 1987).

Hirose and Werger (1987b) calculated the optimal N distribution by means of numerical simulations. However, with a numerical model it is not possible to explicitly define how certain canopy and leaf characteristics may influence the optimal pattern of N distribution. This would be of special interest if plants which differ in their inherent architecture or their modes of photosynthesis are compared. An analytic solution for the optimal N distribution would solve this problem.

In this contribution, we formulate an analytical expression for the optimal N distribution and compare N distribution patterns in dense stands of the four important groups of plants just mentioned: monocotyledonous and dicotyledonous species and species possessing either the C_3 or the C_4 photosynthetic pathways. We specifically investigate the consequences of these patterns of N distribution on the carbon gain in dense stands of these plants by means of numerical calculations of daily canopy photosynthesis.

Materials and methods

Model

Apart from the calculation of the nitrogen distribution, canopy photosynthesis was calculated according to Hirose and Werger (1987a, b) with some of the modifications presented in Schieving et al. (1992b). The mean PFD incident on a leaf at a certain depth (f) in the canopy (I_L) was calculated as:

$$I_L = \frac{I_0 K_L}{(1 - t_L)} \exp(-K_L f) \quad (1)$$

where I_0 is the PFD above the canopy and K_L and t_L the canopy extinction and leaf transmission coefficients for light, respectively (Hirose and Werger 1987b). A list of the most important symbols used is given in Table 1. A non-rectangular hyperbola was used to

Table 1 List of the most important symbols

a_p	Slope of regression of P_m against n_L $\mu\text{mol CO}_2 \text{ m mol N}^{-1} \text{ s}^{-1}$
f	Leaf area index from the top of a canopy m m^{-2}
F_T	Total leaf area index per unit ground area m m^{-2}
I_0	Above canopy photon flux density (PFD) on a horizontal plane $\mu\text{E m}^{-2} \text{ s}^{-1}$
I_L	PFD incident on the surface of a leaf $\mu\text{E m}^{-2} \text{ s}^{-1}$
I_{rL}	Relative incident PFD calculated as I_L/I_0 (dimensionless)
K_L	Coefficient of light extinction (dimensionless)
K_n	Coefficient of nitrogen distribution (dimensionless)
n_{av}	Average leaf N content calculated as N_T/F_T mmol N m^{-2}
n_b	x intercept of regression of P_m against n_L mmol N m^{-2}
n_L	Nitrogen content per unit leaf area mmol N m^{-2}
n_0	Value of n_L at the top of the canopy mmol N m^{-2}
N_T	Total leaf nitrogen per unit ground area mmol N m^{-2}
N_{TF}	Total free nitrogen in the canopy which can be redistributed mmol N m^{-2}
P_g	Gross photosynthesis of a single leaf $\mu\text{mol CO}_2 \text{ m}^{-1} \text{ s}^{-1}$
P_m	Light saturated gross photosynthesis $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
P_n	Net photosynthesis of a single leaf $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
R_d	Dark respiration $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
Φ	Initial slope of the photosynthesis light response curve or quantum yield $\mu\text{mol CO}_2 \mu\text{E}^{-1}$
Θ	Convexity of the photosynthesis light response curve (dimensionless)

formulate the photosynthetic light response curve:

$$P_g = \frac{[(P_m + \Phi I_L) - \{(P_m + \Phi I_L)^2 - 4\Phi\Theta P_m I_L\}^{1/2}]}{2\Theta} \quad (2a)$$

$$P_n = P_g - R_d \quad (2b)$$

where P_g and P_n are the gross and net leaf photosynthetic rate, respectively, P_m the light saturated photosynthesis, R_d the dark respiration and Φ and Θ the curvature factor and quantum yield respectively (Hirose and Werger 1987a). Leaf photosynthesis was related to n_L by assuming linearly increasing relations between P_m , R_d and n_L (Hirose and Werger 1987a):

$$P_m = a_p(n_L - n_b) \quad (3a)$$

$$R_d = a_r(n_L - n_b) + b_r \quad (3b)$$

with a_p and n_b the slope and x intercept of the $P_m - n_L$ relation, a_r the slope of the $R_d - n_L$ relation and b_r the R_d for a leaf with $n_L = n_b$. The quantum yield Φ and curvature factor Θ were assumed to be independent of n_L (Schieving et al. 1992b).

Optimal nitrogen distribution

If the quantum yield Φ and curvature factor Θ are not a function of n_L , it can be proven that if P_m is a linear function of the relative incident PFD I_{rL} ($I_{rL} = I_L/I_0$ in Eq. 1), the N distribution must be optimal (Appendix A).

$$P_m = \alpha I_{rL} \quad (4)$$

where α is a constant. From this condition an expression for the optimal N distribution can be derived (Appendix B).

$$n_L = \frac{K_L N_{TF}}{(1 - \exp(-K_L F_T))} \exp(-K_L f) + n_b \quad (5)$$

with

$$N_{TF} = N_T - n_b F_T \quad (6)$$

where N_T and F_T are the total leaf nitrogen and leaf area index per unit of ground area, respectively. Following Charles-Edwards et al.

(1987), the parameters N_{TF} and n_b (the x intercept of the $P_m - n_L$ relation (Eq. 3a) are regarded as measures for the amount of nitrogen in the canopy that is free for redistribution and the minimum leaf N content, respectively.

Equation 5 shows that the optimal N distribution is a smooth, decreasing function of canopy depth f indicating high n_L at the top and low n_L at the bottom of the canopy. Furthermore, it describes this distribution pattern as a function of four canopy characteristics, namely K_L , F_T , N_T and n_b . It is remarkable to note that optimal pattern of N distribution is not affected by the slope of the $P_m - n_L$ relation (a_p) or by the time distribution of light over the day.

The expression for the optimal N distribution (Eq. 5) presents the opportunity to investigate the effects of K_L , N_T , n_b and F_T on the form of this allocation pattern. To describe this form, Hirose and Werger (1987b) introduced the term "non-uniformity", which signifies the degree in which the upper leaves in the canopy have higher n_L values than the lower ones. Here the non-uniformity of the N distribution is calculated as the absolute difference between the n_L values at the top ($f = 0$ and $n_L = n_0$) and the bottom of the canopy ($f = F_T$ and $n_L = n_{F_T}$). Substituting f in Eq. 5 by 0 and F_T , respectively, and subsequently subtracting the two expressions yields:

$$n_0 - n_{F_T} = K_L N_{TF} = K_L (N_T - F_T n_b) \quad (7)$$

Equation 7 shows that the non-uniformity of the optimal nitrogen distribution increases with K_L and N_T and decreases with n_b and F_T . The effect of K_L is obvious since the N distribution was expected to follow the light distribution (Hirose and Werger 1987b) and a high K_L implies a more attenuated light gradient. Increasing and decreasing the values of N_T and n_b , respectively, implies that more N is available for retranslocation (Eq. 6) and the N distribution would consequently be more non-uniform. The effect of F_T can be explained similarly in that more leaf area implies more leaves requiring a minimum N content n_b which will not be available for redistribution.

Actual nitrogen distribution

The actually measured nitrogen distributions were fitted to an exponential function analogous to the expression for the optimal distribution (Eq. 5):

$$n_L = \frac{K_n N_{TF}}{(1 - \exp(-K_n F_T))} \exp(-K_n f) + n_b \quad (8)$$

where K_n is the coefficient of N distribution. For K_n values approaching zero, Eq. 8 will tend to the uniform N distribution ($n_L = N_T/F_T + n_b$). The optimal distribution is given when K_n equals K_L (i.e. Eq. 8 will be equal to Eq. 5). The degree of non-uniformity of the actual N distribution is characterized in an analogous manner to Eq. 7 by $K_n N_{TF}$.

Methods

Growth of stands

The model was applied to stands of the C_4 monocot [sorghum, *Sorghum bicolor* (L.) Moench cv. Pioneer], the C_3 monocot [rice, *Oryza sativa* (L.) cv. Araure 4], the C_4 dicot [amaranthus, *Amaranthus cruentus* (L.) cv. K113] and the C_3 dicot [soybean, *Glycine max* (L.) Merr.]. A garden experiment was carried out at the Fondo Nacional de Investigaciones Agropecuarias research station in Maracay, Venezuela ($10^{\circ} 15' N$ $67^{\circ} 45' W$; altitude 400 m) on a sandyloam soil. Stands were grown from seed and sowing was done on 18 July 1992 at densities of 125 plants m^{-2} (spacing of 10×8 cm) for *Sorghum*, *Amaranthus* and *Glycine* and 250 plants m^{-2}

(spacing 8×5 cm) for *Oryza*. Fertilization was done with nitrogen (120 kg N ha^{-1} as urea) and phosphorus (50 kg P ha^{-1} as triple superphosphate). Plot size was 2.3×2 m and there were four replicate plots for each species. The day- and night-time temperatures during the growth period were $27\text{--}33^{\circ} C$ and $16\text{--}21^{\circ} C$, respectively.

Stand structure

Canopy structure and light distribution were determined shortly before flowering (76, 45, 52 and 45 days after sowing for *Oryza*, *Sorghum*, *Glycine* and *Amaranthus*, respectively) applying the stratified clipping technique (Monsi and Saeki 1953). We basically followed the method described in Hirose and Werger (1987a). In each plot a 0.8×0.5 m quadrat was established. PFD (400–700 nm) was measured at height increments of 10 cm, for six replicates, with an SF80 line sensor (Decagon Devices Ltd., UK) under an overcast sky. Immediately after each reading, reference PFD at the top of the canopy was recorded. Leaf angles were measured with a protractor.

After light measurements all plants in each quadrat were cut at ground level, put into polythene bags and immediately transported to the laboratory. Here they were clipped every 10 cm along their length, starting from the base, and divided into leaves and stems. Leaf area was measured with a leaf area meter (LI3100, LiCor, USA). Dry weights were determined after oven-drying at $70^{\circ} C$ for 3 days. Organic nitrogen content was determined with a continuous flow analyser (SKALAR, The Netherlands) after Kjeldahl digestion.

Gas exchange measurements

Photosynthesis and dark respiration were measured with a portable open gas exchange system (LCA 2, Analytical Development Co., UK). Calibration of the infra-red gas analyser was achieved using a compressed air cylinder with known CO_2 concentration (349 ppm; Matheson Gas Products Inc.). The humidity sensor was calibrated by letting air pass through a $FeSO_4 \cdot 7H_2O$ column (30 cm long and 5 cm diameter). The quantum sensor was calibrated with a newly calibrated sensor (LI190SA, LiCor). The measuring unit was connected to a Parkinson chamber with an 11 cm^2 window area. The air in the chamber was well mixed by a small fan.

One day after harvesting, photosynthesis measurements were conducted on attached leaves (24 per species) from different heights within the canopy of the remaining plants. Photosynthetic light response curves were constructed by reducing the PFD level from 2000 to $25 \mu E m^{-2} s^{-1}$ by inserting neutral density light filters and by using a clear sky as a light source. R_d was determined for leaves (15 per species) on plants which had been placed in the dark for 1 h. Calculations of gas exchange data and stomatal conductance from raw measurements were carried out according to von Caemmerer and Farquhar (1981). Average leaf temperature (T_L) calculated with an energy balance equation was $31^{\circ} C$ ($\pm 1.5^{\circ} C$). After the gas exchange measurements, the leaves were dried and their nitrogen content was determined by the same procedure as described above.

Results

P_m increased linearly with leaf N content (n_L) in all species (Fig. 1A, B). This increase with N was stronger in C_4 than in C_3 species (higher a_p values; Table 2) portraying the higher PNUE of the C_4 species. The slope values a_p were also slightly higher in the monocot than in the dicot species (Table 2). The x intercepts of the $P_m - n_L$ relation (n_b) were similar in *Oryza*, *Glycine*

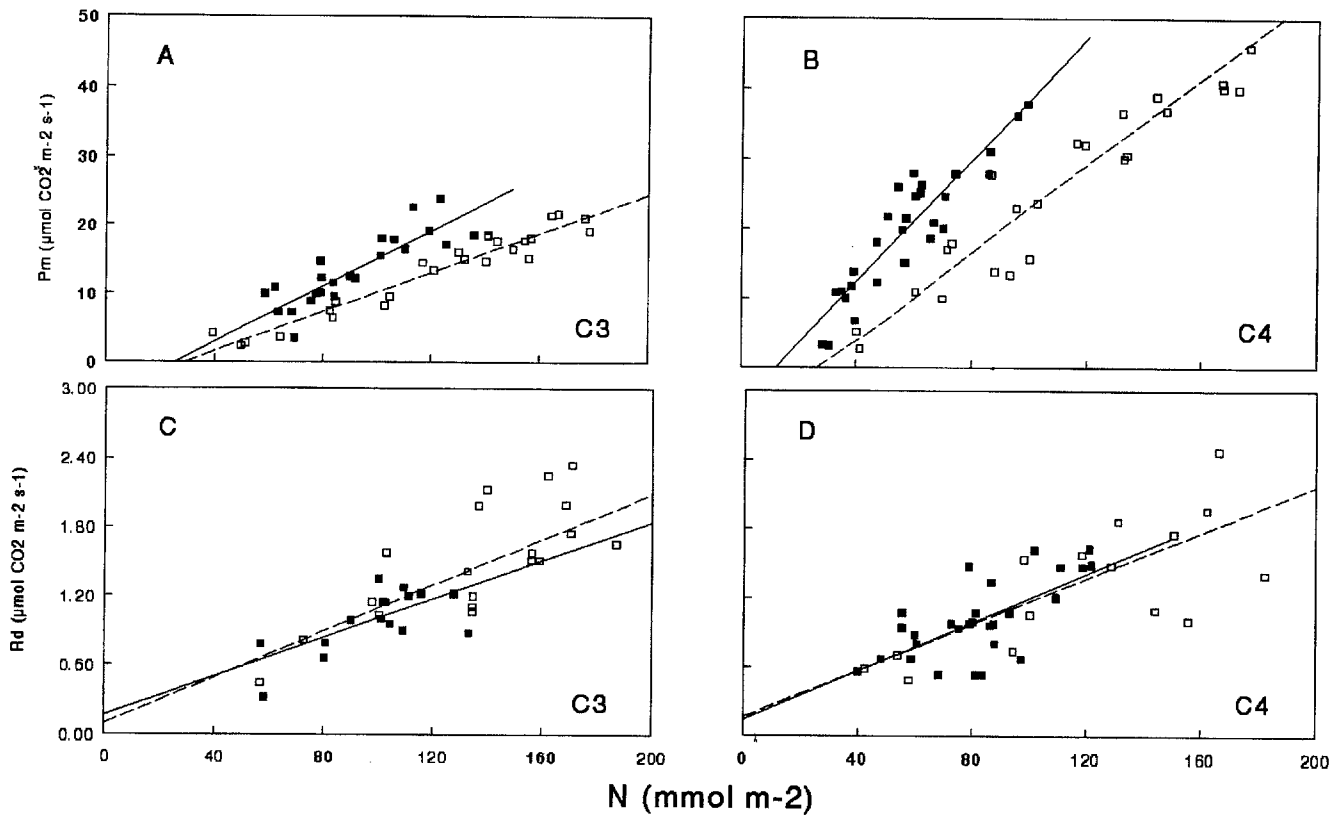


Fig. 1A–D Light saturated rates of photosynthesis P_m (A, B) and dark respiration R_d (C, D) as functions of leaf N content for C_3 (A, C) and C_4 (B, D) monocots and dicots. Open symbols and dashed lines refer to the dicot species *Glycine* (C_3) and *Amaranthus* (C_4), closed

symbols and solid lines to the monocot species *Oryza* (C_3) and *Sorghum* (C_4). Fits were made using Eqs. 3a (P_m) and 3b (R_d). Regression coefficients are given in Table 2

Table 2 The slopes (a_p/a_r , $\text{mmol CO}_2 \text{ mol N}^{-1} \text{ s}^{-1}$) of the relations between light saturated gross photosynthesis (P_m , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and dark respiration (R_d , $\mu\text{mol m}^{-2} \text{ s}^{-1}$) and leaf nitrogen content (n_L , mmol N m^{-2}), the x intercept (n_b , mmol N m^{-2}) of the $P_m - n_L$ relation, the R_d value for $n_L = n_b$ (b_r), the quantum yield (Φ , $\mu\text{mol CO}_2 \mu\text{E}^{-1}$) and the curvature factor (Θ , dimensionless) for C_3 and C_4 mono and dicots

Species	<i>Oryza</i> C_3 monocot	<i>Glycine</i> C_3 dicot	<i>Sorghum</i> C_4 monocot	<i>Amaranthus</i> C_4 dicot
$P_m = a_p(n_L - n_b)$	Eq. 3a			
a_p	0.203	0.143	0.419	0.307
n_b	25.7	29.0	12.5	24.8
r^2	0.786	0.931	0.794	0.89
$R_d = a_r(n_L - n_b) + b_r$	Eq. 3b			
a_r	0.0084	0.0099	0.0110	0.0096
b_r	0.383	0.388	0.284	0.408
r^2	0.461	0.536	0.465	0.486
Φ	0.0431	0.0430	0.0494	0.0500
SEM ($n = 24$)	0.0023	0.0024	0.0011	0.0017
Θ	0.747	0.722	0.855	0.826
SEM ($n = 24$)	0.044	0.024	0.031	0.032

and *Amaranthus* (25.7, 29.0, 24.8 mmol N m^{-2} , respectively) but lower in *Sorghum* (12.5 mmol N m^{-2}). R_d was also linearly related to n_L and ranged from 0.5 to 2 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for all four species (Table 2; Fig. 1C, D). The average measured values for the quantum yield Φ were about 0.043 for the C_3 and 0.050 $\mu\text{mol CO}_2 \mu\text{E}^{-1}$ for the C_4 species (Table 2) The curvature factor Θ was higher in the C_4 (approximately 0.83) than in the C_3 (approximately 0.73) species (Table 2).

The average leaf nitrogen contents ($n_{av} = N_T/F_T$) were lower in the C_4 than in the C_3 species of the same architectural type (Table 3). The monocot stands were found to have higher F_T values than the dicot stands of the same photosynthetic pathway (Table 3). *Glycine* had both greater amounts of total nitrogen (N_T) and greater calculated amounts of free nitrogen N_{TF} (Eq. 6) in the canopy than the other three species (Table 3).

Table 3 Leaf area index (F_T), total canopy nitrogen (N_T), total free nitrogen in the canopy (N_{TF}), average leaf N content (n_{av}) and the extinction coefficient for light (K_L) for C_3 and C_4 monocots and dicots. K_L values were found by fitting Eq. 1 to the data presented in Fig. 2 and corresponding r^2 values are given. Suffixes indicate significant differences between species ($P < 0.05$, Duncan's multiple range test)

Species		F_T $m\ m^{-2}$	N_T $mmol\ m^{-2}$	n_{av} $mmol\ m^{-2}$	N_{TF} $mmol\ m^{-2}$	K_L	
<i>Oryza</i>	C_3 monocot	5.48 ^{ab}	451.4 ^b	82.2 ^b	310.5 ^b	0.469 ^c	$r^2 = 0.959$
<i>Glycine</i>	C_3 dicot	4.76 ^c	540.2 ^a	113.4 ^a	402.2 ^a	0.749 ^a	$r^2 = 0.989$
<i>Sorghum</i>	C_4 monocot	5.92 ^a	394.4 ^c	66.6 ^c	320.3 ^b	0.631 ^b	$r^2 = 0.972$
<i>Amaranthus</i>	C_4 dicot	4.99 ^{bc}	421.8 ^{bc}	84.0 ^b	298.2 ^b	0.779 ^a	$r^2 = 0.978$

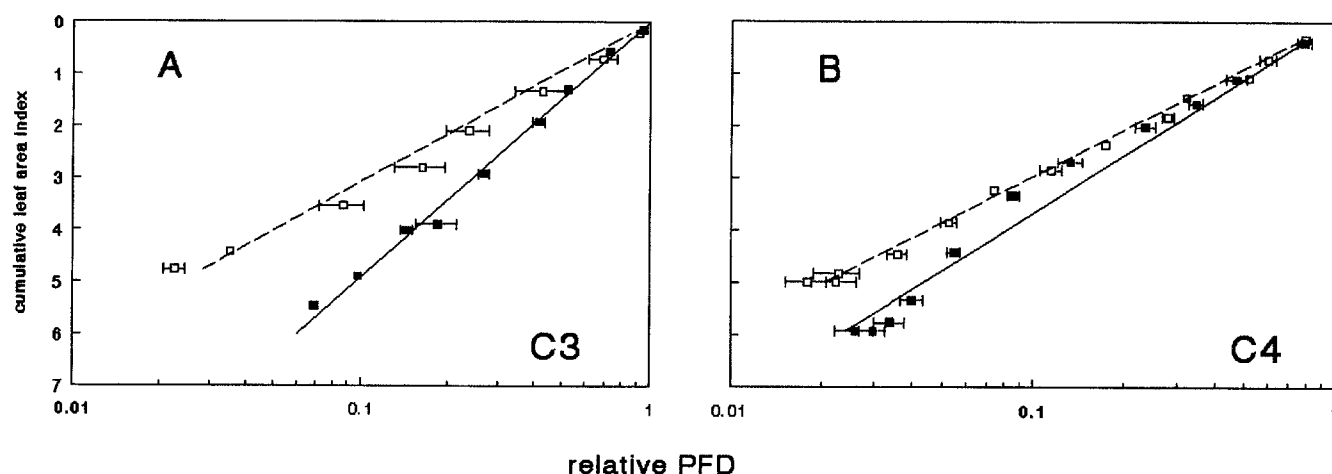


Fig. 2A, B Relative photon flux density (PFD) against cumulative leaf area index in C_3 (A) and C_4 (B) monocots and dicots. For the explanation of the symbols see Fig. 1. Fits were made using Eq. 1.

Regression coefficients are given in Table 3. Bars denote standard errors ($n = 4$)

Table 4 Coefficients of non-uniformity ($mmol\ N\ m^{-2}$) of the optimal ($K_L N_{TF}$: Eqs. 5 and 7) and actually measured ($K_n N_{TF}$: Eq. 8) nitrogen distribution for C_3 and C_4 monocots and dicots. Daily canopy photosynthesis ($mol\ CO_2\ m^{-2}\ day^{-1}$) under the optimal (P_{copt}), the actual (P_{cact}) and uniform (P_{cuni}) N distribution patterns as well as relative and absolute differences between P_{copt} and P_{cuni} were calculated. Suffixes represent significant differences between species ($P < 0.05$, Duncan's multiple range test)

Species		$K_L N_{TF}$	$K_n N_{TF}$	P_{copt}	P_{cact}	P_{cuni}	$P_{cact} - P_{cuni}$
<i>Oryza</i>	C_3 monocot	147.8	44.7 ^b	0.81	0.74	0.65	0.16
	% of P_{copt}				91.4	80.2	
<i>Glycine</i>	C_3 dicot	301.1	119.8 ^a	0.66	0.58	0.41	0.27
	% of P_{copt}				87.8	62.1	
<i>Sorghum</i>	C_4 monocot	202.1	48.0 ^b	1.46	1.25	1.11	0.35
	% of P_{copt}				85.7	76.2	
<i>Amaranthus</i>	C_4 dicot	213.5	119.5 ^a	1.25	1.15	0.85	0.40
	% of P_{copt}				92.0	67.9	

K_L values were higher in the dicot than in the monocot species (Table 3; Fig. 2). *Oryza* had a lower K_L value than sorghum. The dicots also had more horizontally oriented leaves: average leaf angles were 68.5, 31.8, 49.5 and 20.4 in *Oryza*, *Glycine*, *Sorghum* and *Amaranthus*, respectively.

Figure 3 shows the actual (measured) patterns of N distribution in the canopy. All species had non-

uniform N distributions (decreasing n_L values with depth in the canopy). Fitting Eq. 8 to these distributions yielded higher coefficients of non-uniformity $N_{TF} K_n$ in the dicots than in the monocots ($N_{TF} K_n$ values 44.7, 119.8, 48.0 and 119.9 $mmol\ N\ m^{-2}$ for *Oryza*, *Glycine*, *Sorghum* and *Amaranthus*, respectively; Table 4) which shows that the N distribution in the

dicot stands was more non-uniform than in the monocot stands. There were no significant differences in the patterns of N distribution between C₄ and C₃ species of the same architectural type (Table 4; Fig. 3)

Figure 4 shows the calculated optimal patterns of N distribution. In all four species these were more non-uniform than the actual distributions. The non-uniformity coefficients for optimal distributions ($K_{LN_{TF}}$, Eq. 6) are given in Table 4. *Oryza* (C₃ monocot) was calculated to have the most uniform and *Glycine* (C₃ dicot) the most non-uniform optimal nitrogen distribution ($K_{LN_{TF}}$ values 147.8, 301.1, 202.1 and

213.5 mmolN m⁻² for *Oryza*, *Glycine*, *Sorghum* and *Amaranthus*, respectively).

Net daily canopy photosynthesis was computed for actual, optimal and uniform N distributions (Table 4). In all four species photosynthesis at actual distribution was approximately 90% of photosynthesis at optimal distribution. Comparing photosynthesis at optimal to photosynthesis at uniform distribution revealed that the dicots would benefit more from optimizing their N distribution than monocots (gains of 38 and 32% for *Glycine* and *Amaranthus*, respectively, as compared to 20 and 24% for *Oryza* and *Sorghum*, respectively).

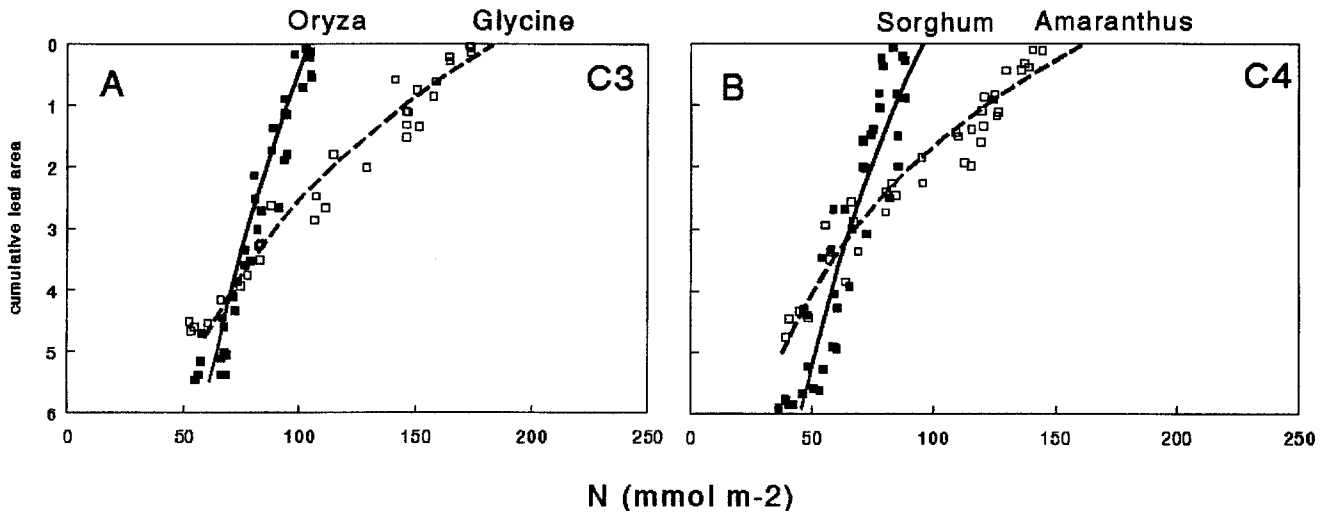
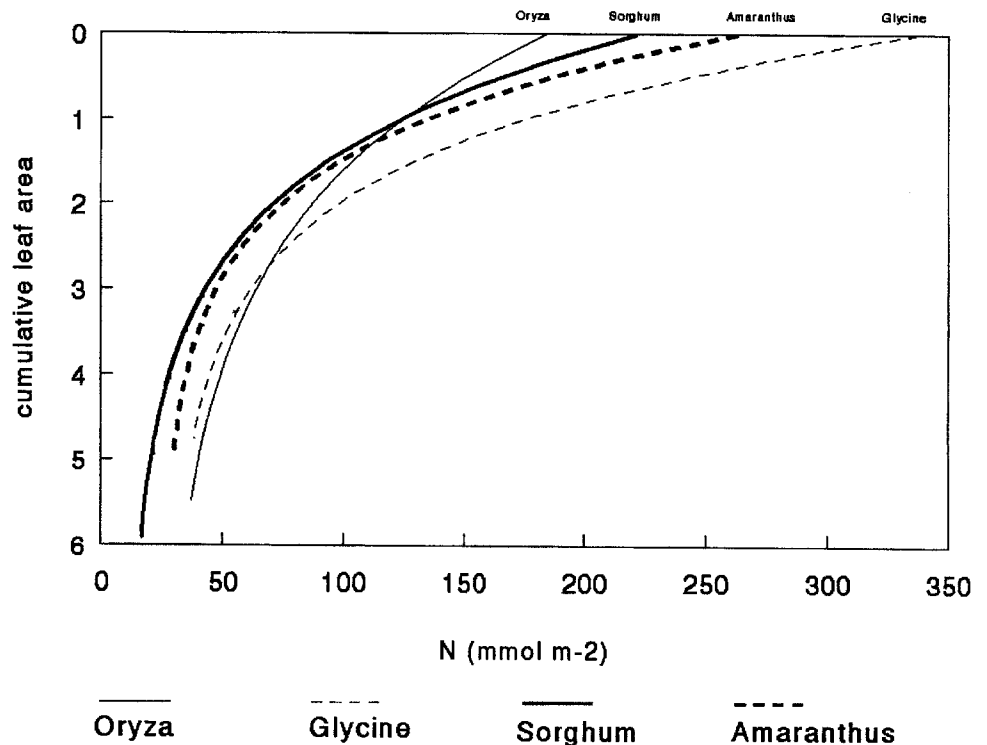


Fig. 3A, B Actual leaf nitrogen distributions in C₃ (A) and C₄ (B) monocots and dicots as a function of cumulative leaf area index.

For explanation of symbols see Fig. 1. Fits were made using Eq. 8. Regression coefficients are given in Table 4

Fig. 4 Patterns of optimal nitrogen distribution as a function of cumulated leaf area index. Parameter values (Eq. 5) are given in Table 4



Discussion

Theoretical model for canopy photosynthesis and nitrogen distribution

From Eqs. 5 and 7 it can be seen that the non-uniformity of the optimal nitrogen distribution increases with K_L and N_T . The slope (a_p) of the relation between P_m and n_L has no effect on the form of the optimal N distribution (Eq. 5) in that stands of species with different a_p values but similar in all other respects have identical optimal N distributions. It should be noted however that Eqs. 5 and 7 are only descriptions of the form of the optimal N distribution and that no clue is given with regards to the effects of this optimization on photosynthesis. In order to assess this effect, daily canopy photosynthesis was calculated under the optimal (P_{copt}) and uniform N distributions (P_{cuni}) (Fig. 5). The difference between these two rates of photosynthesis ($P_{\text{copt}} - P_{\text{cuni}}$) was regarded as a measure for the photosynthetic benefit resulting from optimization of the N distribution. Figure 5A gives the values of P_{copt} and P_{cuni} and the difference ($P_{\text{copt}} - P_{\text{cuni}}$) as a function of K_L , while Fig. 5B and C describes these three as a function of total canopy nitrogen N_T . In Fig. 5B and C the a_p value of the $P_m - n_L$ relation was also different (a_p was 0.2 in Fig. 5B and 0.4 in Fig. 5C).

The increase in canopy photosynthesis resulting from optimizing the N distribution ($P_{\text{copt}} - P_{\text{cuni}}$) increases strongly with the value of K_L (Fig. 5A) indicating that the importance of nitrogen redistribution increases in stands with high K_L values. Regarding the nitrogen availability (N_T), it can be seen that the difference ($P_{\text{copt}} - P_{\text{cuni}}$) increases and then decreases with N_T . Apparently, there is a value of N_T at which the photosynthetic benefit of optimizing the N distribution is maximal. From Fig. 5B and C it can be seen that this value of N_T depends on the a_p value of the $P_m - n_L$ relation. These figures illustrate that at low nitrogen availability (low N_T) a dense stand of a photosynthetically efficient species (high a_p ; Fig. 5C) would benefit more from optimizing its N distribution than a stand of an inefficient species (low a_p ; Fig. 5B) while at high N_T the reverse holds true.

In the model a linear relation between P_m and n_L was assumed (Eq. 3a). This was in accordance with the findings in this (Fig. 1; Table 2) as well as various other studies (Hirose and Werger 1987a; Sage and Pearcy 1987; Pons et al. 1989; Schieving et al. 1992a, b). Some authors (Evans 1989; Field and Mooney 1986) however found curvilinear relations at high n_L . Pons et al. (1989) suggested that in the case of the optimal N distribution, extrapolation of the linear $P_m - n_L$ relation to the high n_L values calculated for the top of the canopy would lead to unrealistically high P_m values. In this study the highest P_m values calculated for the optimal N distribution were 32.5, 44.3, 86.7 and 66.2 $\mu\text{mol CO}_2$

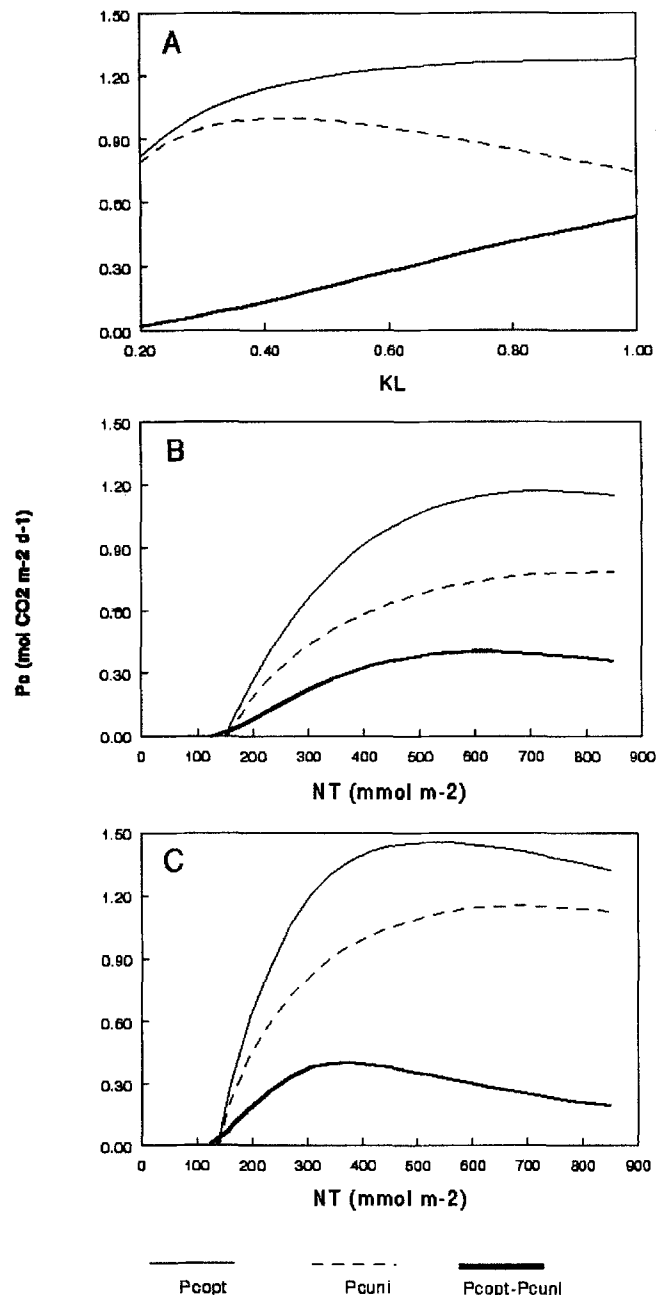


Fig. 5A–C Daily canopy photosynthesis (P_c) under optimal (P_{copt} , solid line) and uniform nitrogen (P_{cuni} , dashed line) distribution, as well as the difference between the two ($P_{\text{copt}} - P_{\text{cuni}}$, heavy solid line), against canopy extinction coefficient for light (A) and total canopy nitrogen (B, C). The slope of the relation between light saturated photosynthesis and nitrogen was changed from 0.2 (B) to 0.4 (C) $\mu\text{mol CO}_2 \text{ s}^{-1} \text{ mmol N}^{-1}$. Unless further specified the canopy characteristics of *Amaranthus* (Table 3) were assumed

$\text{m}^{-2} \text{ s}^{-1}$ for *Oryza*, *Glycine*, *Sorghum* and *Amaranthus*, respectively. These values were 2 times greater than the highest values measured in the field. However, P_m values of 60 and 80 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ have been measured in C_3 and C_4 desert ephemerals, respectively

(Pearcy and Ehleringer 1983) indicating that the P_m values calculated in the present study probably do not exceed a theoretical upper limit of photosynthesis.

Experimental stands of C_3 and C_4 mono- and dicotyledonous species

In all four species the actual patterns of nitrogen allocation were more uniform than the optimal ones. The calculated canopy photosynthesis was approximately 10% lower than the maximal value (Table 4). Pons et al. (1989) listed a number of aspects which might explain the deviation of actual from optimal. Environmental factors such as drought, herbivory or photo-inhibition at high PFD may cause plants to maintain n_L values in the top of the canopy which are lower than optimal. In the present study the metabolic costs of nitrogen allocation are not accounted for, although these may impose a substantial carbon cost in comparison with the gain resulting from nitrogen allocation (Field 1983). These factors would tend to favour N reallocation patterns which are more uniform than the optimal ones (Pons et al. 1989).

The dicot species with their more horizontal leaves formed stands with higher K_L values than the monocot species (Fig. 2; Table 3). The dicot stands also had more non-uniform patterns of N distribution (Fig. 3; Table 4) which was predicted by Eq. 7. It was further calculated that the photosynthetic benefits related to N redistribution were greater in dicots than in monocots (Table 4). Apparently, a clear relation exists between canopy structure as a result of plant architecture and the vertical pattern of N distribution. Species with more horizontally oriented leaves produce stands with high K_L values resulting in a more attenuated light climate, and will therefore reallocate more nitrogen towards the top of the canopy in order to enhance their photosynthetic performance.

The most striking difference between the C_4 and C_3 species that were studied here appears to be the higher slope values a_p of the $P_m - n_L$ relation in the C_4 species (Fig. 1; Table 2) illustrating their higher PNUE. Such results were also found in various other studies (Brown 1978; Sage and Pearcy 1987) and can be explained on the basis of the C_4 concentrating mechanism (Osmond et al. 1982). Between monocot and dicot species of the same photosynthetic pathway, it was found that monocots had higher a_p values (Fig. 1; Table 2). However, such differences are not generally found between monocot and dicot species (Poorter et al. 1990). The x intercept of the $P_m - n_L$ relation (n_b) was lower for *Sorghum* than for the three other species (Table 2). The n_b value, however, is determined by the amount of nitrogen which is invested in processes other than photosynthesis (Pons et al. 1989) and will probably not depend on the possession of either the C_3 or C_4 photosynthetic pathway. Thus, Sage and Pearcy

(1987) found similar n_b values in a C_3 and a C_4 dicot. The average leaf N content (n_{av}) was lower in the C_4 than in the C_3 species, which was in accordance with former studies (Brown 1978; Sage and Pearcy 1987).

The measured nitrogen distributions were similar between the C_3 and C_4 species of the same architectural type. This was in accordance with the model presumption that this pattern of distribution is not a function of differences in the slope of the relation between P_m and n_L . More generally, the results from this paper strongly suggest that the pattern of nitrogen distribution is mainly determined by the light extinction rate and the total amount of free nitrogen in the canopy.

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Appendix A

In a canopy with a fixed total amount of nitrogen N_T , daily canopy photosynthesis P_c is maximized if at every depth f in the canopy we have:

$$\frac{dP_{day}(I_L, n_L)}{dn_L} = \sigma \quad (A1)$$

where P_{day} is the daily carbon gain of a leaf, n_L the nitrogen content per unit leaf area, I_L the photon flux density (PFD) incident on a leaf and σ the Lagrange multiplier (Field 1983). P_{day} is given by the daily integral of net leaf photosynthesis (P_n ; Eq. 2b):

$$\frac{dP_{day}(I_L, n_L)}{dn_L(f)} = \int_0^{t_D} \left[\frac{dP_g(I_L, n_L)}{dn_L(f)} - \frac{dR_d(n_L)}{dn_L(f)} \right] dt \quad (A2)$$

where t and t_D are the solar time and daylength, respectively, R_d the leaf dark respiration and P_g gross leaf photosynthesis (Eq. 2a). If R_d is linearly related to n_L (Eq. 3b), we may write

$$\int_0^{t_D} \frac{dR_d(n_L)}{dn_L(f)} = a_r t_D \quad (A3)$$

with a_r the slope of the $R_d - n_L$ relation. Equation A3 is constant with canopy depth f . Equation 2a can be rewritten as:

$$\begin{aligned} P_g(I_L, n_L) &= P_m(n_L) \frac{(1+x) - [(1+x)^2 - 4\Theta x]^{1/2}}{2\Theta} \\ &= P_m(n_L) y(x) \end{aligned} \quad (A4)$$

with

$$x(t, f) = \frac{\Phi I_L(t, f)}{P_m(n_L)} \quad (A5)$$

where Φ and Θ are the quantum yield and curvature factor respectively, P_m the light saturated rate of leaf photosynthesis and $y(x)$ the ratio P_g/P_m . P_m is a linear function of n_L (Eq. 3a) so that its

derivative to n_L is a_p . By substituting P_m in Eq. A2 by Eq. A4 we can now write

$$\begin{aligned} \frac{d}{dn_L(f)} y(x) P_m(n_L) &= \frac{dy(x)}{dx} \frac{dx}{dP_m} \frac{dP_m}{dn_L} P_m + y(x) \frac{dP_m}{dn_L} \\ &= \left[\frac{dy(x)}{dx} \left(-\frac{\Phi I_L}{P_m^2} \right) P_m + y(x) \right] a_p \\ &= \left[y(x) - x \frac{dy(x)}{dx} \right] a_p \end{aligned} \quad (\text{A6})$$

If we take P_m as a linear function of relative incident PFD (I_{rL})

$$P_m(n_L) = \alpha I_{rL}(f) \quad (\text{A7})$$

where α is a constant and

$$I_{rL}(f) = \frac{I_L(t, f)}{I_0(t)} \quad (\text{A8})$$

with I_0 the PFD at the top of the canopy, we find for Eq. A5:

$$x(t, f) = \frac{\Phi I_0(t) I_{rL}(f)}{\alpha I_{rL}(f)} = \frac{\Phi I_0(t)}{\alpha} = x^*(t) \quad (\text{A9})$$

The resulting value of x (i.e. $x^*(t)$) is independent of f . Substitution of Eqs. A3, A6 and A9 into Eq. A2 gives:

$$\frac{dP_{\text{day}}(I_L, n_L)}{dn_L(f)} = \int_0^{t_0} \left[\left(y(x^*) - x^*(t) \frac{dy(x^*)}{dx^*(t)} \right) a_p \right] dt - a_t t_D \quad (\text{A10})$$

which is constant at every depth f in the canopy and hence the expression which defines the optimal nitrogen distribution is given by Eq. A7.

Appendix B

We derive an analytical expression for the optimal N distribution assuming the condition set in Eq. 4. If light saturated photosynthesis P_m is a linear function of both leaf nitrogen content (n_L) and relative incident photon flux density (PFD) I_{rL} ($I_{rL} = I_L/I_0$; see Appendix A and Eq. 1) i.e.

$$P_m = a_p(n_L - n_b)$$

and

$$\begin{aligned} P_m &= \alpha I_{rL} \\ &= \alpha \frac{K_L}{(1 - t_L)} \exp(-K_L f) \end{aligned}$$

then we can find by eliminating P_m :

$$n_L - n_b = \frac{\alpha K_L}{a_p(1 - t_L)} \exp(-K_L f) \quad (\text{B1})$$

where α is a constant, a_p and n_b are the slope and x intercept of the $P_m - n_L$ relation, K_L and t_L are the canopy extinction and leaf transmission coefficients and f is the canopy depth expressed as cumulated leaf area index. At the top of the canopy $f = 0$, and hence:

$$P_m = \frac{\alpha K_L}{(1 - t_L)} = a_p(n_0 - n_b) \quad (\text{B2})$$

with n_0 the leaf N content at the top of the canopy. Solving for α gives:

$$\alpha = a_p \frac{(1 - t_L)(n_0 - n_b)}{K_L} \quad (\text{B3})$$

and substituting Eq. B3 into Eq. B1 yields:

$$n_L - n_b = (n_0 - n_b) \exp(-K_L f) \quad (\text{B4})$$

Total free nitrogen N_{TF} can be calculated by integration of Eq. B4 over canopy depth, yielding:

$$N_{TF} = (n_0 - n_b) \frac{(1 - \exp(-K_L F_T))}{K_L}$$

where F_T is the total leaf area index and

$$n_0 - n_b = \frac{K_L N_{TF}}{(1 - \exp(-K_L F_T))} \quad (\text{B5})$$

Substituting Eq. B5 into Eq. B4 yields the optimal nitrogen distribution:

$$n_L = \frac{N_{TF} K_L}{(1 - \exp(-K_L F_T))} \exp(-K_L f) + n_b \quad (\text{B6})$$

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