

Leaf senescence and resorption as mechanisms of maximizing photosynthetic production during canopy development at N limitation

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Summary

1. A canopy N distribution model optimizing photosynthesis was combined with mechanisms for senescence and N resorption to predict canopy leaf area index (LAI) development as a function of canopy nutrient content, N_c .
2. Shedding of leaves at the bottom of the canopy was initiated when it increased canopy photosynthesis, through resorption and redistribution of N from lost leaves. The amount of N resorbed was modelled as a fraction (R_f) of the N in the leaf prior to senescence.
3. For a fixed N_c , the LAI at which leaf shedding was initiated was calculated for different R_f s for canopies of *Amaranthus cruentus*, *Glycine max*, *Oryza sativa* and *Sorghum bicolor*.
4. Predicted LAIs exceeded optimal LAIs estimated without leaf shedding and N resorption. LAI increased with increasing R_f . For all four species, the model closely predicted the observed LAIs with $R_f = 0.7$.
5. Area-based resorption efficiency increased and litter N concentration decreased with increasing LAI and average canopy N concentration (mol N m^{-2} leaf). A reduction of R_f , e.g. in response to increased soil N availability, decreases resorption efficiency.
6. The model provides a mechanistic basis for interpreting plant nutrient–resorption–LAI relations.

Key-words: Canopy N distribution, litter production, optimal LAI model, resorption efficiency

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Introduction

It is widely believed that maximization of net photosynthesis (gross photosynthetic rate – dark respiration rate) drives the development of many plants. Consequently, many formulations of optimal canopies have been based on optimization of photosynthesis with respect to different plant properties, such as leaf nutrient concentration (e.g. Field 1983); leaf area per leaf mass (SLA, e.g. Schieving & Poorter 1999); and canopy leaf area per ground area (LAI, e.g. Anten *et al.* 1995a). This study explores the consequences for canopy development of adding two connected processes, senescence and nutrient resorption.

Because photosynthesis is strongly dependent on tissue nutrient concentration, particularly N, and irradiance, the distribution of N in the canopy with respect to light should be an important plant property. Field (1983) proposed an optimal canopy N distribution, where N is distributed such that no transfer of N

between different positions in the canopy increases canopy net photosynthesis. This leads to leaf N concentrations proportional to the irradiance. This hypothesis has been tested many times and, although it does not fully explain the observations, it is a main determinant for canopy N distribution in many plants (e.g. Anten, Schieving & Werger 1995b; Field 1983; Hirose & Werger 1987b).

For a given amount of canopy N, it is possible to calculate the optimal LAI, i.e. the LAI that maximizes photosynthesis. Theoretical predictions of optimal canopy LAI and experimental measurements were compared by Anten *et al.* (1995a), who found that observed canopy LAIs were larger than predicted for a given amount of canopy N. A possible explanation for these results, suggested by Schieving & Poorter (1999), was that higher LAI and lower N concentration than optimal results from competition between plants differing in SLA. However, none of the above-mentioned studies includes leaf senescence or N resorption as optimizing processes. The question is, how will these processes affect plant properties such as N concentration, LAI and resorption efficiency?

Nutrient resorption during leaf senescence is often expressed as nutrient resorption efficiency (fraction of N resorbed at senescence relative to green leaf N concentration) or resorption proficiency, the lowest litter N concentration that can be reached by resorption (Killingbeck 1996). A complete understanding of the controlling factors is lacking, and their relation to plant nutrient status is unclear (Aerts 1996). In a review of many studies, Aerts (1996) found both positive and negative relations between resorption efficiency and plant N concentration within groups of plants of the same type (e.g. deciduous trees). The only significant relation between resorption efficiency and N concentration was a positive one for forbs. Unfortunately, resorption has rarely been studied in relation to canopy properties such as LAI and N distribution.

The aim of this study was to combine the concept of optimal canopy N distribution with simple mathematical descriptions of principles for the onset of leaf senescence and N resorption. Implications for relations between plant N concentration, LAI and resorption efficiency were investigated.

Theory and model

SINGLE LEAF PHOTOSYNTHESIS MODEL

Single leaf photosynthetic rate (P) is given by the standard nonrectangular hyperbola (e.g. Hirose & Werger 1987a)

$$P = \frac{I\phi + P_{\max} - \sqrt{(I\phi + P_{\max})^2 + 4\theta I\phi P_{\max}}}{2\theta} - R \quad \text{eqn 1}$$

$$P_{\max} = p(N - N_{\min}) \quad \text{eqn 2}$$

$$R = r(N - N_{\min}) + R_{\min} \quad \text{eqn 3}$$

where P_{\max} (light-saturated photosynthetic rate) and R (dark respiration rate) are assumed to be linearly related to N (amount of N per unit leaf area) above some minimum N (N_{\min} ; Hirose & Werger 1987a). The quantum yield, ϕ , and curvature factor, θ , are assumed independent of N (Schieving, Werger & Hirose 1992). Although this study is focused on N distribution, the model would also apply for phosphorus (P) in case of P limitation. All symbols and units are given in Table 1.

OPTIMAL CANOPY N DISTRIBUTION

An optimal canopy N distribution is obtained when N is distributed such that no transfer of N between different positions in the canopy increases canopy photosynthesis (P_c ; Field 1983). This can be formulated as:

$$\frac{d}{dz} \left(\frac{dP}{dN} \right) = 0 \quad \text{eqn 4}$$

where leaf photosynthesis (P) is a function of N and photon flux density (PFD), I (eqn 1), and N and I are functions of the cumulative LAI from the top of the canopy (z). Thus canopy depth (z) and total extent (W) are defined solely by cumulative LAI. PFD incident on a leaf, I , is assumed to depend on z according to:

$$I(z) = I_0 e^{-kz} \quad \text{eqn 5}$$

where I_0 is the PFD above the canopy and k is the canopy light extinction coefficient.

Table 1. List of symbols

Symbol	Definition	Units
P	Leaf photosynthetic rate	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
P_{\max}	Light-saturated gross photosynthetic rate	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
P_c	Whole canopy photosynthetic rate	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
P_{bottom}	P at bottom of canopy	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
R	Dark respiration	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
I	PFD incident on the surface of a leaf	$\mu\text{mol m}^{-2} \text{ s}^{-1}$
I_0	PFD above the canopy on a horizontal plane	$\mu\text{mol m}^{-2} \text{ s}^{-1}$
k	Canopy light extinction coefficient	$\text{m}^{-2} \text{ m}^2$
N	Leaf N concentration	mmol N m^{-2}
N_{av}	Average canopy N	mmol N m^{-2}
N_c	Total canopy N per ground area	mmol N m^{-2}
N_{\min}	x intercept of regression of P_{\max} against N	mmol N m^{-2}
N_L	Litter N	mmol N m^{-2}
N_{bottom}	N at the bottom of the canopy	mmol N m^{-2}
W	Canopy LAI	$\text{m}^2 \text{ m}^{-2}$
ϕ	Quantum yield	$\mu\text{mol CO}_2 \mu\text{mol}^{-1}$
θ	Convexity of the P - I relation curve	–
p	Slope of regression of P_{\max} against N	$\mu\text{mol CO}_2 (\text{mmol N})^{-1} \text{ s}^{-1}$
r	Slope of regression of R against N	$\mu\text{mol CO}_2 (\text{mmol N})^{-1} \text{ s}^{-1}$
R_{\min}	R at $N = N_{\min}$	$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$
Rf	Fraction N resorbed at senescence	–
Rf^*	Resorption function that leaves a constant N_L	–

Given that total canopy LAI is W and total canopy nitrogen is N_c , eqn 4 can be solved for N to give the optimal N distribution:

$$N(z) = \frac{k(N_c - N_{\min}W)e^{-kz}}{1 - e^{-kW}} + N_{\min} \quad \text{eqn 6}$$

which means that, as functions of canopy depth (z), N is linearly related to I . This result is also valid for other expressions for P , given certain conditions on the form of P (Sands 1995).

Total canopy photosynthetic rate, P_c , is given by:

$$P_c = \int_0^W P(N(z), I(z)) dz \quad \text{eqn 7}$$

CONDITION FOR LEAF SHEDDING

Retranslocation of N ensures an optimal N distribution and a maximization of photosynthesis (P_c) for a fixed amount of canopy N (N_c) and LAI (W). However, as the canopy grows, PFD and P at the bottom of the canopy decline. At some W and N_c it becomes possible to further increase P_c if the lowest leaf is shed and part of the N optimally redistributed in the remaining canopy. The condition for this is that the increase in P_c from resorbed N from the shed leaf ($P_{c,\text{gain}}$) exceeds the photosynthesis of the lost leaf (P_{lost}). For an infinitesimal amount of leaf loss, dW_{loss} , this can be formulated as:

$$\frac{dP_c}{dW_{\text{loss}}} = \frac{dP_{c,\text{gain}}}{dW_{\text{loss}}} - \frac{dP_{\text{lost}}}{dW_{\text{loss}}} = \frac{dP_c}{dN_c} \frac{dN_c}{dW_{\text{loss}}} - P_{\text{bottom}} = \frac{dP}{dN} N_{\text{bottom}} \cdot Rf - P_{\text{bottom}} > 0 \quad \text{eqn 8}$$

Rf is a resorption function that defines the fraction of N resorbed at senescence. Because of the optimal N distribution dP_c/dN_c is equal to dP/dN . N_{bottom} and P_{bottom} refer to N (eqn 6) and P (eqn 1) at $z = W$.

From eqn 8, a value of W when litter formation is initiated can be calculated for a given amount of canopy nitrogen, N_c . This W is the maximum LAI the plant can reach for the given N_c . Thus the LAI is assumed to increase until it is constrained by litter formation. The optimal LAI for a given N_c , if the plant adjusts its LAI to maximize P_c without forming litter (or forming litter without losing N), is obtained by using $Rf = 1$ in eqn 8. $Rf = 0$, on the other hand, corresponds to the case where no N is resorbed and no leaf is shed until its net photosynthesis becomes negative.

Because eqn 8 defines maximal W as a function of N_c , an optimal plant canopy – the coupled W and N_c that maximizes total canopy photosynthesis (P_c) – can be derived from:

$$dP_c/dN_c = 0 \quad \text{eqn 9}$$

CALCULATIONS AND DATA

By solving eqn 8 numerically for W for a range of values of canopy N (N_c), the relationship was analysed between N_c and LAI (W) at the point where litter starts

Table 2. Parameter values (from Anten *et al.* 1995a). k is the measured extinction coefficient of the canopy nitrogen distribution (k_N)

Parameter	<i>Amaranthus cruentus</i>	<i>Glycine max</i>	<i>Oryza sativa</i>	<i>Sorghum bicolor</i>
I_0	1000	1000	1000	1000
k	0.402	0.298	0.144	0.222
ϕ	0.0500	0.0430	0.0431	0.0494
θ	0.826	0.722	0.747	0.855
p	0.307	0.143	0.203	0.419
r	0.0096	0.0099	0.0084	0.0110
R_{\min}	0.408	0.388	0.383	0.284
N_{\min}	24.8	29.0	25.7	12.5

to form. From the resulting relation between W and N_c , the mean N concentration in the canopy ($N_{\text{av}} = N_c/W$), litter N concentration (N_L) and N resorption efficiency $[(N_{\text{av}} - N_L)/(N_{\text{av}})]$ were calculated. N_L was calculated from N at the bottom of the canopy (eqn 6, where $z = W$) and the resorption fraction, Rf , i.e. $N_L = N(W) \cdot (1 - Rf)$. The calculations were performed for different constant values of Rf as well as for a different resorption function Rf^* . Rf^* is defined to always leave the same N concentration in litter (N_L) independently of current leaf N . This corresponds to a constant resorption proficiency. Parameter values from Anten *et al.* (1995a) were used (Table 2).

Contrary to the prediction of the optimal canopy theory (eqns 5, 6) the measured extinction coefficients for PAR (k_L) and canopy N (k_N) are not equal. However, instantaneous incident PAR on a leaf (I) and k_L are highly variable in time, while k_N should reflect the effective PAR distribution integrated over a time relevant for the response of the canopy N distribution. Thus, we use the measured k_N as k in our calculations.

Results

CANOPY N-LAI RELATIONS

Figure 1 shows how the growth of the canopy leaf area (W) is constrained by litter formation (W_L curve) as a function of total canopy N (N_c). Nitrogen uptake is not modelled explicitly, but the balance between N uptake and growth determines where W reaches W_L and litter formation starts. A higher N uptake rate relative to leaf area growth rate means that litter formation starts at a larger W than for a lower N uptake/growth ratio. The growth of W will continue along the W_L curve, with simultaneous production of leaves and litter. If N uptake is less than that lost in litter, W will decrease along the W_L curve. The calculation of W_L is based on the assumption of a dense canopy with constant light extinction (k), an assumption not relevant for small plants, that is, for W and N_c approaching zero.

Increasing the resorbed fraction of N at senescence (Rf) decreases W for a given N_c (Fig. 2) and increases canopy mean N concentrations (N_{av}) for a given W (Fig. 3). The maximal Rf , $Rf = 1$, corresponds to

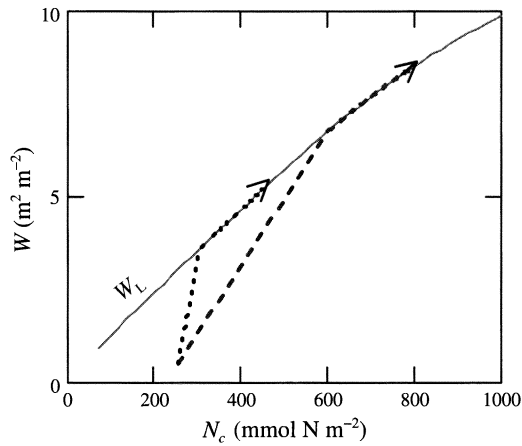


Fig. 1. Possible growth trajectories of LAI (W) constrained by litter formation according to W_L as a function of total canopy N, N_c . The dotted line represents growth of W at a lower N-uptake/growth ratio than the dashed line. Resorption fraction, $Rf = 0.7$. Parameters for *Amaranthus cruentus* (Table 2).

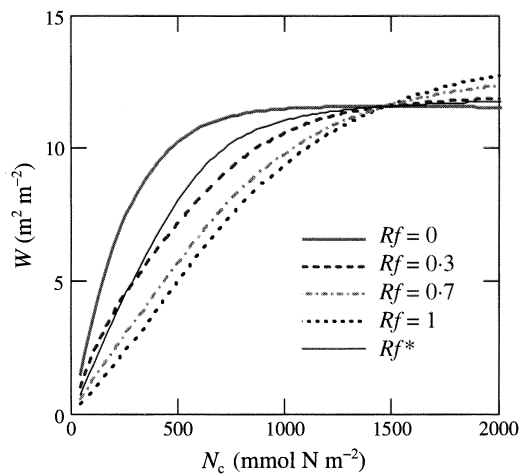


Fig. 2. Litter formation-constrained LAI (W ; cf. W_L in Fig. 1) as a function of total canopy N, N_c . Rf is the resorption fraction and Rf^* is resorption defined by constant litter N concentration, $N_L = N_{min}$. Parameters for *Amaranthus cruentus* (Table 2).

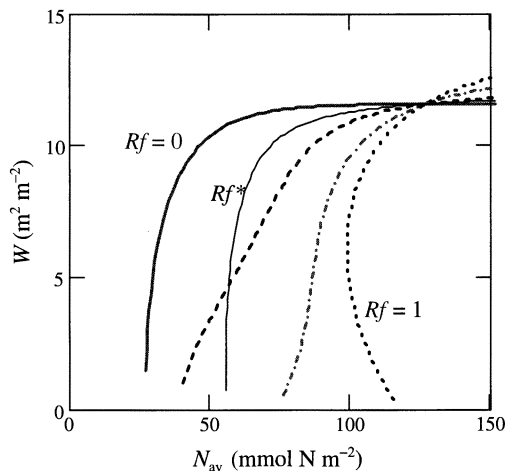


Fig. 3. Litter formation constrained LAI (W) vs average canopy N concentration, N_{av} . Parameters for *Amaranthus cruentus* (Table 2); lines as in Fig. 2.

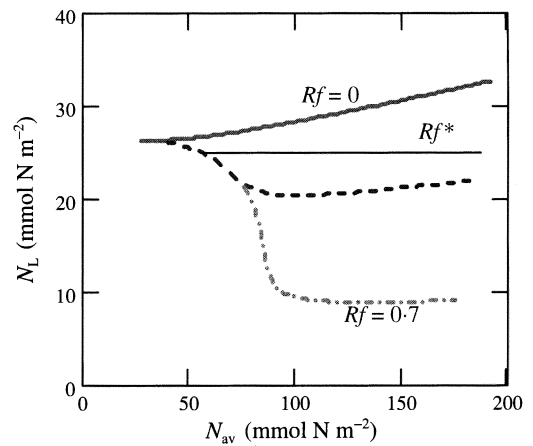


Fig. 4. Litter N concentration, N_L vs average canopy N concentration, N_{av} . Parameters for *Amaranthus cruentus* (Table 2); lines as in Fig. 2. $Rf = 1$ is not included because it means that $N_L = 0$ or that no litter is produced.

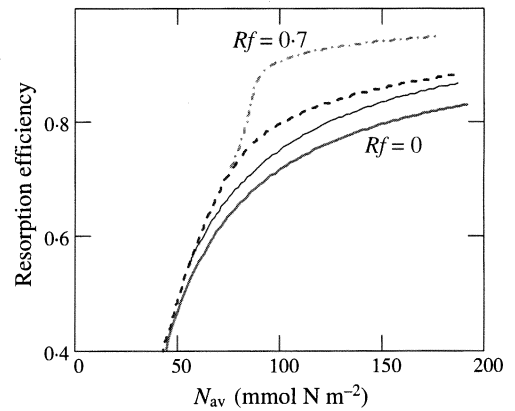


Fig. 5. Resorption efficiency vs average canopy N concentration, N_{av} . Parameters for *Amaranthus cruentus* (Table 2); lines as in Fig. 2. $Rf = 1$ is not included because that all litter N is resorbed.

resorption of all N, which is equal to optimizing a static W for a fixed N_c without invoking litter production (eqn 8). This means that plants constrained by the suggested principle of senescence have canopies with larger LAI than would be optimal for a given amount of canopy N in a static canopy. The curves in Figs 2 and 3 intersect at the point where $dP/dN = 0$ (eqn 8) and $dP_c/dN_c = 0$ (eqn 9). This point represents the optimal plant canopy in terms of N_c and W – no canopy can have a larger canopy photosynthesis, P_c . This point should be an upper limit to canopy LAI, and increases in N_c or W beyond this point will not be dealt with in the following discussion.

The model was also tested with a different type of resorption regulation, Rf^* , defined by a constant litter N concentration (N_L), i.e. a constant resorption proficiency. Different values of N_L were analysed, but only the curves for the maximum possible $N_L = N_{min}$ are shown in Figs 2–5. Larger predefined N_L s are not possible because the leaf N concentration at the bottom of the canopy approaches N_{min} at large LAIs, and the N_L must be less than the leaf N concentration.

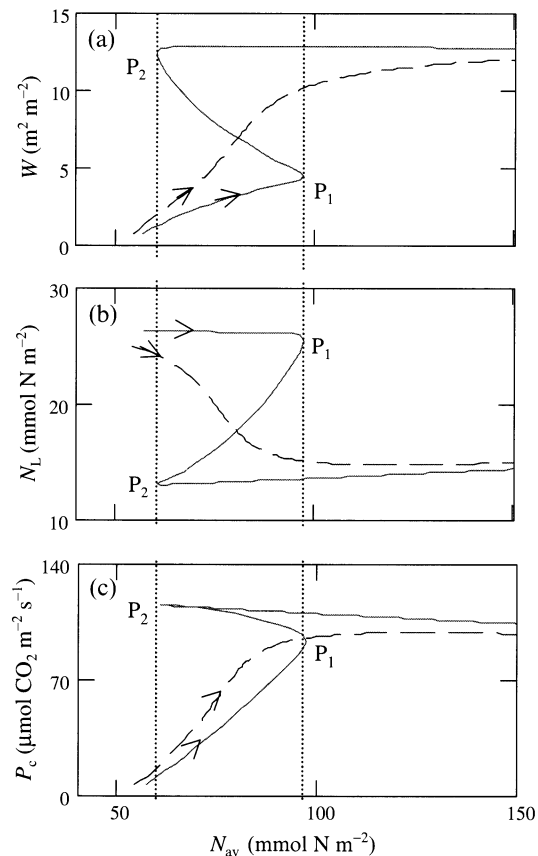


Fig. 6. Canopy properties vs average canopy N concentration at litter formation-constrained W for a Blackman ($\theta = 1$; solid line) and a normal ($\theta = 0.826$; dashed line) leaf photosynthesis light response. (a) Canopy LAI (W); (b) litter N concentration (N_L); (c) canopy photosynthesis (P_c). Arrows indicate the direction of change as W increases. For the Blackman curves, point P_1 corresponds to a shift from N limitation to light limitation; point P_2 corresponds to W at maximum canopy photosynthesis. Resorption fraction, $Rf = 0.5$. Parameters for *Amaranthus cruentus* (Table 2).

LITTER N CONCENTRATION AND RESORPTION EFFICIENCY

Litter N concentration (N_L) is, over large ranges, related negatively to average canopy N concentration, N_{av} (Fig. 4), which seems counterintuitive. This is a consequence of the complex relation between N_{av} , N_L and W (eqn 8), where W and N_{av} affect N_L in opposite directions. The slope of the relation between N_{av} and W reflects their relative limiting effect on canopy photosynthesis (P_c), where W determines the canopy light interception. To further explore these results in relation to the relative N and intercepted light (PAR) limitation of leaf photosynthesis (P), a Blackman photosynthetic response ($\theta = 1$, causing a distinct shift between light- and N-limited P) was tested. The litter formation-constrained growth of W , N_{av} , N_L and P_c was derived as described above for a Blackman and a normal ($\theta = 0.826$) photosynthesis response curve (Fig. 6). The transition from results representative for a 'normal' response curve ($\theta < 1$) to results representative for the Blackman response occurs for θ very close to 1.

At point P_1 in Fig. 6, P of the Blackman response shifts from N limitation to light limitation, and P cannot be increased by a further increase in leaf N ; N then remains at the breakpoint between N and light limitation, which is shifted towards lower N as the light interception per leaf is reduced with increasing W . To maintain the optimized canopy N distribution, the reduction in N is greatest at the bottom of the canopy. Because litter is formed at the bottom of the canopy, this leads to a reduction in litter N concentration (Fig. 6b). For the normal response curve, as W increases, the gradual change from N to light limitation reduces bottom leaf N , but not mean canopy N (N_{av}). Thus the simultaneous reduction in N_L and increase in N_{av} is caused by the differential change in N at lower and upper levels of the canopy during a gradual transition from N limitation to light limitation of leaf photosynthesis.

When W reaches point P_2 in Fig. 6, canopy photosynthesis (P_c) is saturated with respect to both canopy N and W (intercepted PAR). Further increase in canopy N reduces P_c , due to increased respiration.

As a consequence of the negative relation between mean canopy N (N_{av}) and litter N (N_L), there is a positive relationship between area-based resorption efficiency and N_{av} . The increase is greater the larger the Rf , although the slopes of the relation are quite flat except for low canopy N concentrations (Fig. 5).

Discussion

Anten *et al.* (1995a) found that monospecies canopy LAIs were larger than optimal canopy LAIs predicted by maximization of canopy photosynthesis (cf. $Rf = 1$ in Figs 2 and 7). Schieving & Poorter (1999) proposed an explanation where competition between species of different SLA results in an evolutionary stable LAI higher than the optimal LAI. We present here an alternative explanation that does not rely on assumptions of multispecies competition to shape the canopy. Instead of being a direct result of optimization of photosynthesis at given levels of resources, LAI grows until it is constrained by litter formation. LAI may then be constant, although new leaves and litter are formed, and plant height and shape may change. This continuous growth of the canopy height is a means of competing for light. New leaves are formed in the top, while bottom leaves receive less light, become less productive, and eventually are shed. However, N cannot be redistributed from old to new leaves without losses, unless resorption is complete (cf. $Rf = 1$, eqn 8). Thus under N-limited conditions LAI is a result of a dynamic process, and not solely of optimization of photosynthesis at a fixed amount of canopy N.

Comparing the model predictions of the relationship between LAI (W) and canopy N (N_c) with the experimental results by Anten *et al.* (1995a) for four different plant species (*A. cruentus*, *Glycine max*, *Oryza sativa* and *Sorghum bicolor*) and high- and low-N treatments

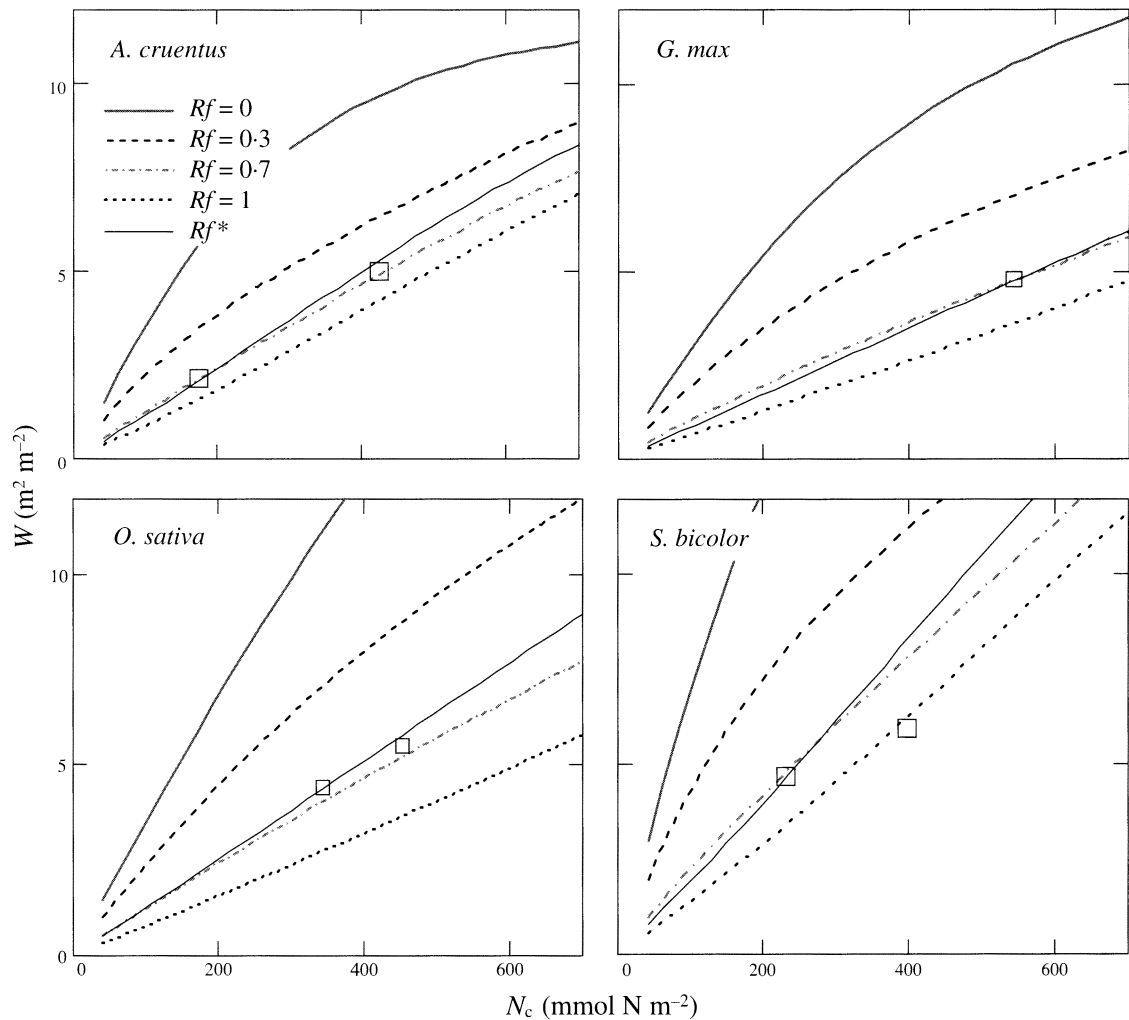


Fig. 7. Litter formation-constrained LAI (W) vs. canopy N, N_c , for different species (Table 2). Squares are measured values at different N treatments from Anten *et al.* (1995a). Rf^* has been chosen for best fit to data and corresponds to litter N concentrations $N_L = 17.4, 23.1, 20.3, 9.25$ for *Amaranthus cruentus*, *Oryza sativa*, *Glycine max* and *Sorghum bicolor*, respectively.

shows that, for all species and treatments except one, the LAI values lie almost exactly on the predicted curve for resorption factor $Rf = 0.7$ (Fig. 7). The deviant, *S. bicolor* at high-N treatment, should not be seen as a deviation from the model prediction; rather, it may be caused by such a high N availability relative to growth rate that the observed LAI occurs at an N concentration where litter formation is not yet beneficial (cf. Figure 1), below the $Rf = 0.7$ curve in Fig. 7. The lines for Rf^* (constant litter N concentration) fit the observed change in canopy LAI between high- and low-N treatment slightly less well than the curves for resorption fraction (Rf). Furthermore, significantly different values of Rf^* are required for fitting the different species in Fig. 7.

This study has focused on changes in N and LAI at constant irradiance (I_0) and light extinction coefficient, k . Changes in k can be used to represent different plant densities – a lower density leads to more light dispersing between plants, reducing k . Halving k (Fig. 8) shows that for small plants with $Rf \geq 0.7$, the effect on W is marginal, although the effect is larger for higher

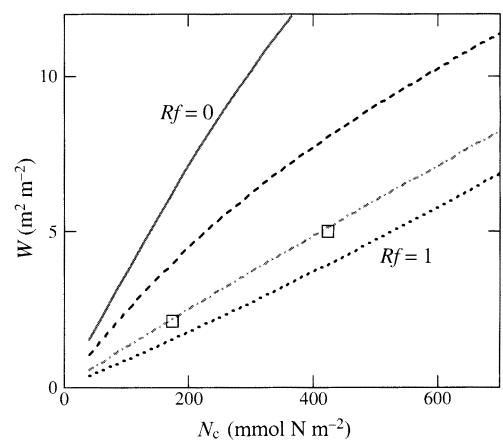


Fig. 8. Litter formation-constrained LAI (W) vs. canopy N, N_c , for *Amaranthus cruentus* but with light-extinction parameter $k = 0.2$; cf. Figure 7 with $k = 0.4$. Lines as in Figs 2 and 7.

N_c and LAI, when light limitation increases in importance. In accordance with this prediction for small plants, Bazzaz & Harper (1977) found that leaf senescence in *Linum usitatissimum* was initiated at a

constant plant biomass of 13 g for equally sized pots, independent of planting density. Furthermore, they found that the biomass at initiation of senescence was increased only by addition of nutrients, which is also predicted by our model (Fig. 1).

Area-based resorption efficiency is predicted to increase with LAI and N_{av} , which seems to have been observed only for forbs (Aerts 1996). This could indicate that additional processes and metabolic costs associated with senescence and N retranslocation (Field 1983) play a more important role for other plant types, such as trees.

If these costs are comparable to costs for N uptake, it could be hypothesized that the different costs and benefits of N acquisition should be balanced. Furthermore, assuming that N resorption costs increase with increasing resorption fraction (Rf), another possible relation between N resorption efficiency and N availability emerges. A reduction in soil N availability would increase N acquisition costs, leading to an increase in Rf . This implies a negative relation between plant N concentration and resorption efficiency. However, because an increase in plant N concentration N_{av} and an accompanying decrease in Rf are seen to change resorption efficiency in different directions (Fig. 4), it is difficult to predict the combined effect. This could be one explanation for the wide variation in observed resorption efficiency and its relation to nutrient status (Aerts 1996; Killingbeck 1996). Furthermore, estimation of mass-based resorption efficiency is complicated by changes in SLA accompanying changes in N per area (N). If the predicted variation in N was entirely due to variation in SLA, our mass-based resorption efficiency would be equal to $Rf = 0.7$ independently of mean canopy N.

Other factors that influence resorption efficiency could be seasonal climate changes, leaf age and non-leaf nutrient pools. In a resorption model of Kull & Kruijt (1999), plant N and C are separated between leaves and a nonleaf common pool, and where resorption depends on the transfer between these pools. They conclude that herbaceous species have a small common pool compared to trees, implying that our model is more appropriate for herbs.

In conclusion, senescence and resorption should be viewed as properties of the canopy, rather than at the level of single leaves. Although the present model represents a highly simplified view of a plant, the suggested principles provide a simple mechanistic basis for interpreting observed N–resorption–LAI relations under N-limited conditions. The model should be applicable for single-species herbaceous plant canopies.

Additional factors, such as costs of resorption, probably should be invoked to gain further insight into, for example, N availability–resorption relations in trees.

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