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Maximization of Daily Canopy Photosynthesis: Effects of Herbivory on Optimal Nitrogen Distribution

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Recent models have shown that higher leaf nitrogen concentration per unit area maximizes nitrogen use efficiency with increasing light intensity. As a result, total canopy photosynthesis is maximized when nitrogen concentrations are higher towards the top of a canopy. Expanding upon this previous work, a model of daily canopy photosynthesis was constructed based on distributions of light, leaf nitrogen, and folivory. The model indicates that the optimal distribution of nitrogen depends significantly upon both the severity and location of folivory. Relative to nitrogen distributions that maximized daily canopy photosynthesis without herbivory, the optimal nitrogen distribution shifted towards either more uniform or skewed distributions when herbivores fed on high nitrogen foliage at the top of the canopy or on low nitrogen foliage towards the bottom of the canopy, respectively.

These results suggest that, because foliar losses are balanced by increased irradiance of remaining leaves, plants' nitrogen allocation patterns should depend on how severe defoliation is and whether damage is concentrated towards the top or bottom of a canopy. Moreover, the critical importance of nitrogen distribution to photosynthesis implies that plants should not necessarily minimize loss of leaf area to folivores, but should protect the ratio of total nitrogen to leaf area and the distribution of nitrogen within the canopy. As a corollary to the nutrient stress hypothesis of plant defense theory, the model suggests that plants may need to translocate nutrients to maintain an optimal distribution in the canopy following herbivory. The model reinforces the point that leaf area loss alone is a poor indicator of loss of photosynthetic capacity when nitrogen is non-uniformly distributed among leaves. To accurately assess damage to a plant, one must consider not only what resources have been removed, but what resources remain.

1. Introduction

Maximization of photosynthesis by a plant is likely to occur with a non-uniform distribution of nitrogen within the canopy. This is because at high light levels, such as those at the top of a canopy, light is unlikely to be limiting and photosynthetic capacity will be strongly correlated with leaf nitrogen content (Mooney *et al.*, 1981; Field & Mooney, 1986). On the other hand, at low light levels, such as those at the bottom of a canopy, increasing leaf nitrogen would yield only small photosynthetic gains because photon interception is limiting (Björkman, 1981) and because maintenance requirements and carbon losses during darkness are relatively greater (Gulmon & Chu, 1981). Thus, total canopy photosynthesis is maximized when nitrogen concentrations are higher towards the top of a canopy (Field, 1983).

In a model of daily canopy photosynthesis, Hirose & Werger (1987b) demonstrated that the specific distribution of nitrogen that maximizes daily canopy photosynthesis varies according to canopy density and the nitrogen pool available for allocation among leaves. The optimal concentration of nitrogen in leaves in the uppermost part of the canopy was found to increase with increasing canopy density and total canopy nitrogen. Because the model assumes that total canopy nitrogen and canopy density are fixed within a plant, the effects of changes in nitrogen and

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canopy density on photosynthesis were compared only between plants having different canopy densities and nitrogen allocation patterns.

A single plant, however, may experience changes in total nitrogen and leaf area as a consequence of herbivory. Leaf removal will decrease the total nitrogen and leaf area within a canopy, but simultaneously will increase the amount of light penetrating to lower levels. Photosynthesis subsequently will be reduced by nitrogen losses, and increased by greater light availability to remaining leaves. The precise balance of costs and benefits of leaf removal to daily canopy photosynthesis will depend on the nitrogen distribution within the canopy and the position of foliage that is lost to herbivory. As a result, the nitrogen distribution which maximizes canopy photosynthesis prior to herbivory does not necessarily maximize photosynthesis after herbivory, and the optimal distribution of nitrogen among leaves within a canopy likely will depend on the severity and location of photosynthetic tissue losses, and the degree to which a plant can compensate for lost photosynthetic tissue.

Here, a model is presented that examines the distribution of nitrogen that maximizes canopy photosynthesis in the presence of herbivores. This model expands upon that of Hirose & Werger (1987*b*), but is novel in that it includes effects of herbivory. Several feeding rules for herbivores are formulated and the optimal nitrogen allocation pattern, i.e. the nitrogen distribution that maximizes canopy photosynthesis, is determined. The model predicts that optimal nitrogen distribution in a canopy will depend upon the position of foliage removed within the canopy and on the intensity of herbivory.

2. The Model

The model begins by assuming a plant that has some pre-existing distribution of nitrogen within its canopy (specified by K_a; see below), and that generalized herbivores remove horizontal layers of foliage from the top, middle, or bottom of the canopy. The amount of foliage removed depends on whether the herbivore's foraging "goal" is to consume a fixed amount of nitrogen, or to consume a fixed leaf area or leaf mass. The rules governing foliage removal are not intended to mimic any particular type of herbivore but are intended to test the effects of a broad range of leaf removal patterns. The overall level of photosynthesis will be diminished by herbivory because leaf nitrogen is removed, but will be increased in remaining foliage below regions of leaf removal because of greater light penetration. The suppression of photosynthesis will not be identical for all nitrogen distributions because different nitrogen distributions will result in removal of different leaf areas or different amounts of nitrogen. In this model, the daily canopy photosynthesis of the new canopy after attack is compared with that of a plant which suffered attack by identical herbivores, but which had a different initial nitrogen distribution.

The model consists of four parts. The first part determines nitrogen concentration of leaves at different levels in the canopy. The second part determines how herbivory affects the nitrogen distribution and light penetration through the canopy. The third part calculates irradiance of leaves at different canopy depths. The fourth part calculates net photosynthesis (carbon exchange rate) per unit leaf area as a function of irradiance, nitrogen concentration, and dark respiration. Integration of net photosynthesis over all depths for a 24-hr period yields daily net photosynthesis in the canopy. Parts 1, 3, and 4 are adapted directly from Hirose & Werger (1987b); part 2 is novel. Symbol definitions are provided in Appendix A.

2.1. NITROGEN DISTRIBUTION AMONG LEAVES WITHIN A CANOPY

The leaf nitrogen content per unit area, N_L, at a particular leaf area index (depth from the top of the canopy) F within the canopy is given by

$$N_L = N_0 \exp(-K_a F/F_t). \tag{1}$$

Total leaf nitrogen per unit ground area (N_t) is given by the integral of leaf nitrogen over all depths in the canopy:

$$N_t = \int_0^{F_t} N_L \, dF = N_0 F_t (1 - e^{-K_a})/K_a, \tag{2}$$

where N_0 is the leaf nitrogen content per unit area at the top layer of the canopy, and F_t is the total leaf area index (leaf area per unit ground area). K_a is the coefficient of leaf nitrogen allocation, and determines how N_t is apportioned throughout F_t. The canopy has a uniform distribution of nitrogen when $K_a = 0$, so that every leaf has a nitrogen concentration equal to the mean. As K_a increases ($K_a > 0$), the nitrogen distribution becomes skewed so that leaves at the top of the canopy have higher concentrations than lower leaves.

N_0 is defined as

$$\begin{aligned} N_0 &= K_a N_t/F_t/(1 - e^{-K_a}) \qquad K_a \neq 0 \\ N_0 &= N_t/F_t \qquad\qquad\qquad\quad K_a = 0. \end{aligned} \tag{3}$$

2.2. HERBIVORE FEEDING RULES

Either no leaves were removed, or herbivores removed foliage in accordance with one of two feeding criteria:

Nitrogen removal. Herbivores consume foliage until some nitrogen requirement (N_R) is met. Nitrogen is limiting to the growth of many herbivores, insects in particular (White, 1978; Mattson, 1980; Scriber, 1984), and hence can be important in determining food choice. To approximate the severity of leaf removal typically found in nature, this requirement leads to removal of 0–20% of the total canopy nitrogen (N_t). On average, herbivores consume about 2·5% of the net production of temperate deciduous forests and 12% of that in old field habitats (Wiegert & Owen, 1971).

Leaf area removal. Herbivores remove foliage until a leaf area requirement (L_R) is satisfied. Leaf area removal may be translated into consumption of a particular leaf mass because specific leaf weight (leaf dry weight per unit leaf area) is assumed to be constant. L_R ranges between 0–20% of total leaf area.

Nitrogen and leaf area removal clearly are not mutually exclusive events because consuming nitrogen necessitates reduction of leaf area, and vice versa. However, because of different nitrogen distributions, consumption of a particular amount of leaf area can lead to a wide range of amounts of nitrogen being consumed. Hence, nitrogen and leaf area removal require different accounting procedures and therefore are considered separately, expressed as percentages of total nitrogen and leaf area for convenience in comparing their effects. The model does not require that herbivores be sensitive to the proportion of nitrogen or leaf area that is removed.

Feeding may occur in the top, bottom, or middle of the canopy. Nitrogen and leaf area removal "goals" may each be achieved by following one of four rules (equations are presented in Table 1):

A. Top of Canopy

1. *Nitrogen goal.* Foliage with the highest nitrogen content is consumed first, followed by progressive consumption of foliage of lower nitrogen concentration until the nitrogen requirement is fulfilled. More formally, all foliage from depth 0–F is removed to satisfy the nitrogen requirement N_R as defined in Table 1, where N_L is the leaf nitrogen per unit area at a particular leaf area depth F from the top of the canopy, and F_t is the total leaf area index.

2. *Leaf area goal.* Foliage at the top of the canopy is consumed first, and foliage deeper into the canopy is then progressively removed until the leaf area requirement is met. Thus, L_R is the amount of foliage removed from leaf area depth 0–F such that it equals F, the leaf area index (Table 1).

TABLE 1

Feeding rules that determine the amount and position of foliage that is removed from the canopy. See Appendix A for definitions of variables

Goal	Description	Formula	Conditions
Nitrogen	Top of canopy (Rule A1)	$N_R = \int_0^F N_L \, dF$	$(0 \leq F \leq F_t)$
	Bottom of canopy (*Rule B1*)	$N_R = \int_F^{F_t} N_L \, dF$	$(0 \leq F \leq F_t)$
	Middle of nitrogen distribution (Rule C1)	$N_R = \int_{F_i}^{F_j} N_L \, dF$	$0{\cdot}3N_t = \int_0^{F_t} N_L \, dF$ $(0 \leq F_i \leq F_j \leq F_t)$
	Middle of leaf area distribution (Rule D1)	$N_R = \int_{0{\cdot}3F_t}^{F_j} N_L \, dF$	$(0{\cdot}3F_t \leq F_j \leq F_t)$
Leaf area	Top of canopy (Rule A2)	$L_R = F$	$(0 \leq F \leq F_t)$
	Bottom of canopy (Rule B2)	$L_R = F_t - F$	$(0 \leq F \leq F_t)$
	Middle of nitrogen distribution (Rule C2)	$L_R = F - F_i$	$0{\cdot}3N_t = \int_0^{F_t} N_L \, dF$ $(F_i \leq F \leq F_t)$
	Middle of leaf area distribution (Rule D2)	$L_R = F - 0{\cdot}3F_t$	$(0{\cdot}3F_t \leq F \leq F_t)$

Rules A1 and A2 mimic the behavior of herbivores that prefer high nitrogen foliage or feed at the top of a canopy where nitrogen concentration is greatest.

B. Bottom of canopy

1. *Nitrogen goal.* Foliage containing the lowest concentration of nitrogen is consumed, with progressive consumption of foliage of higher nitrogen concentration until the nitrogen requirement is fulfilled.

2. *Leaf area goal.* Starting at the bottom of the canopy, foliage is progressively consumed, working higher up into the canopy until the leaf area requirement is met.

Rules B1 and B2 are appropriate for herbivores that consume foliage from the bottom of a canopy where nitrogen concentration is lowest. Many herbivores, for example vertebrate browsers, are restricted to feeding on the lower branches of trees simply because higher branches are out of reach, but within this restricted range may be sensitive to nutritional quality (Löyttyniemi, 1981).

C. Middle of nitrogen distribution

1. *Nitrogen goal.* Consumption of foliage beginning near the middle of the canopy nitrogen distribution progresses with consumption of foliage that is further from the canopy top until the nitrogen requirement is met. The herbivores are assumed to begin feeding at a depth in the canopy where 30% of the total nitrogen resides in higher levels.

2. *Leaf area goal.* Consumption of foliage beginning near the middle of the canopy nitrogen distribution progresses with consumption of foliage deeper into the canopy until the leaf area requirement is satisfied. Herbivores are assumed to start feeding at a depth where 30% of the total canopy nitrogen resides in higher levels.

Rule C1 is a compromise between Rules A1 and B1, whereas Rule C2 is a compromise between Rules A2 and B2. Feeding towards the middle of a canopy may be preferred to feeding at the top or bottom of a canopy where risks of exposure to predators and harsh environmental conditions may be greater.

D. Middle of leaf area distribution

1. *Nitrogen goal.* Consumption of foliage begins near the middle of the canopy leaf area distribution and progresses deeper into the canopy until the nitrogen requirement is satisfied. This rule is similar to Rule C1 except that the depth at which feeding begins is fixed at a depth where 30% of the total leaf area lies in higher levels.

2. *Leaf area goal.* Consumption of foliage begins near the middle of the leaf area distribution and progresses deeper into the canopy until the leaf area requirement is met. Herbivores are assumed to start feeding at a depth where 30% of the total leaf area lies in higher levels of the canopy.

In each of the above scenarios, whichever of nitrogen or leaf area removal that is not set to a constant by a feeding rule varies according to the nitrogen distribution with the canopy. It is important to note that the distribution of nitrogen is assumed to be fixed during herbivory, i.e. there is no transport of nitrogen.

2.3. PENETRATION OF LIGHT THROUGH A CANOPY

The light intensity (photon flux density or PFD) on the surface of a leaf at leaf area index (LAI) value F from the canopy top is designated as I_t, and is an expansion of Beer's law (Monsi & Saeki, 1953) described by an exponential function of F:

$$I_t = I_0 K_t \exp(-K_t F)/(1-m), \qquad (4)$$

where I_0 is the PFD on a horizontal plane just above the canopy surface, K_t is the extinction coefficient of light, and m is the leaf transmission coefficient (Saeki, 1960). Irradiance is adjusted for foliage removal by setting light attenuation to zero over regions devoid of leaves.

A squared sine curve (Takenaka, 1986) describes the change over a 24-hr period in PFD above the canopy:

$$I_0 = \hat{I}_0 \sin^2[\pi (t-6)/12] \qquad (6 \leqslant t < 18)$$
$$I_0 = 0 \qquad (0 \leqslant t < 6, 18 \leqslant t < 24), \qquad (5)$$

where t is the solar time (hr) and $\hat{I}_0$ is the PFD at noon ($t = 12$).

2.4. PHOTOSYNTHESIS (CARBON EXCHANGE RATE)

A non-rectangular hyperbolic function was used to fit the light response curve of photosynthesis (Johnson & Thornley, 1984; Hirose & Werger, 1987*a*, *b*):

$$\ominus P_g^2 - (\phi I_t + P_{max}) P_g + \phi I_t + P_{max} = 0,$$

which expands to

$$P_g = [\phi I_t + P_{max} - \{(\phi I_t + P_{max})^2 - 4\ominus\phi I_t P_{max}\}^{1/2}]/2\ominus, \qquad (6)$$

where P_g, gross photosynthesis, is net photosynthesis plus dark respiration; I_t is the PFD on the leaf; P_{max} is the gross photosynthesis at saturating PFD. ϕ indicates the initial slope of the curve (quantum yield), and $\ominus$ is a dimensionless parameter that

TABLE 2
Parameter units and values used in the model. Values are from Hirose & Werger (1987a, b) for Solidago altissima

Parameter	Units	Value
m	—	0·086
K_t	—	0·613
K_a	—	0·798
F_t	$m^2\,m^{-2}$	4·24
N_t	$g\,m^{-2}$	5·62
a_r	$\mu mol\ (CO_2)\ m^{-2}\,sec^{-1}$	0·120
b_r	$\mu mol\ (CO_2)\ g^{-1}\ (N)\ sec^{-1}$	0·346
a_m	$\mu mol\ (CO_2)\ m^{-2}\,s^{-1}$	−7·86
b_m	$\mu mol\ (CO_2)\ g^{-1}\ (N)\ sec^{-1}$	12·5
a_p	—	0·0211
b_p	$m^2\,g^{-1}\ (N)$	0·0188
a_t	—	1·10
b_t	$m^2\,g^{-1}\ (N)$	−0·251
I_0	$\mu E\,m^{-2}\,sec^{-1}$	1000·00

provides the convexity of the curve. Net photosynthesis (the carbon exchange rate) is gross photosynthesis (P_g) minus dark respiration (R):

$$P = P_g - R. \tag{7}$$

The light response of net photosynthesis is determined by N_L (the leaf nitrogen concentration per unit area) via linear regressions (Appendix B).

Daily canopy carbon exchange rate (P_{day}, daily canopy photosynthesis) is found by integration of leaf photosynthesis at all depths within a canopy over a 24-hr period, and is of the form:

$$P_{day} = \int_0^{24} \int_0^{F_t} P(F, t)\,dF\,dt. \tag{8}$$

Following Hirose & Werger (1987*b*), parameter values used in equations 1-17 are for *Solidago altissima* (Table 2). Note that $F_t = 4{\cdot}24$ and $N_t = 5{\cdot}62$ are reference values that were altered when comparing effects of herbivory under different canopy densities.

3. Results

3.1. NO HERBIVORY

With no herbivory, predictions were identical to those described by Hirose & Werger (1987*b*) and Hirose *et al.* (1988). Daily canopy photosynthesis at first increased with increasing values of K_a above 0, but then declined as nitrogen became more concentrated in the top of the canopy (Fig. 1). As canopy density increased but mean nitrogen concentration per unit area remained constant, the K_a that maximized daily canopy photosynthesis increased. The photosynthesis response curve for $N_t = 5{\cdot}62$ and $F_t = 4{\cdot}24$ (total nitrogen and total leaf area, respectively) that is maximal with nitrogen distribution specified by $K_a = 1{\cdot}3$ will be used as a reference throughout the paper.

3.2. HERBIVORY CAUSING A SHIFT TOWARDS MORE UNIFORM OPTIMAL NITROGEN DISTRIBUTIONS

If herbivores attack high-nitrogen foliage at the top of a canopy, then a shift in the optimal nitrogen distribution towards a more uniform allocation of nitrogen is predicted. At all nitrogen distributions tested, removal of high-nitrogen foliage reduced total canopy photosynthesis from levels achieved without herbivory. A plant with nitrogen distributed according to a K_a value of 1·3 experienced a 22% reduction in photosynthesis following removal of 20% of the canopy nitrogen (Table 3, Rule A1). A plant with nitrogen distributed according to a K_a value of 0·9 experienced only a 13% reduction in photosynthesis and as a result had the highest daily canopy photosynthesis when 20% of the canopy nitrogen was removed. Consumption of fixed amounts of high-nitrogen foliage (Rule A1) resulted in a shift of the optimal K_a towards smaller values, indicating that daily canopy photosynthesis was maximized by a more uniform nitrogen distribution than under conditions of no herbivory (Fig. 2). The extent of this shift increased with increasing severity of defoliation.

The optimal K_a was reduced much more severely when a particular percentage of leaf area was removed from the canopy top than when an identical percentage of total nitrogen was removed (Fig. 2). In

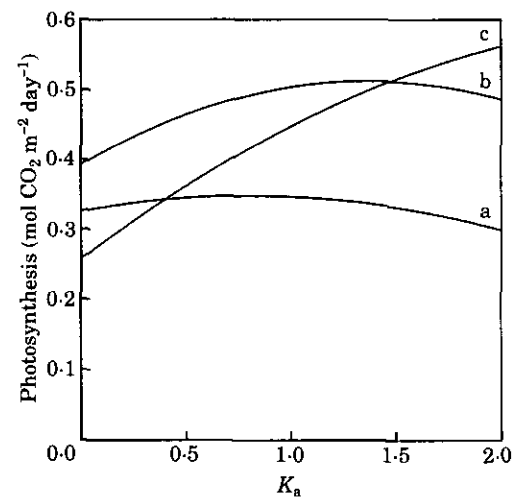

FIG. 1. Daily canopy photosynthesis as a function of nitrogen distribution pattern (coefficient of nitrogen allocation, K_a) with no herbivory. (a) Total leaf area $F_t = 2{\cdot}1\ m^2\,m^{-2}$, total canopy nitrogen $N_t = 2{\cdot}81\ g\,m^{-2}$; (b) $F_t = 4{\cdot}24$, $N_t = 5{\cdot}62$ (used as reference curve); (c) $F_t = 8{\cdot}48$, $N_t = 11{\cdot}24$.

TABLE 3

Optimal nitrogen distributions ($K_{a\,max}$) and changes in net canopy photosynthesis as a function of nitrogen distribution and herbivory. Change in photosynthesis due to herbivore damage is for 20% leaf area or nitrogen removal, and is expressed as a percentage of photosynthesis achieved with $K_a = 1{\cdot}3$ and no herbivory

Herbivore goal	Feeding rule	Location of damage	$K_{a\,max}$	Change in photosynthesis	
				$K_a = 1{\cdot}3$	$K_{a\,max}$
None	—	—	1·3	—	—
Nitrogen	A1	Top	0·9	−21·8	−12·8
	B1	Bottom	3·1	−2·9	+37·0
	C1	Middle	1·0	−9·7	−7·2
	D1	Middle	1·1	−11·8	−9·5
Leaf area	A2	Top	0·5	−30·6	−13·0
	B2	Bottom	2·1	−1·9	+36·8
	C2	Middle	0·9	−14·3	−9·7
	D2	Middle	1·1	−10·6	−8·9

addition, removal of a given percentage of the leaf area from the upper part of the canopy caused a greater reduction in photosynthesis than did removal of the same percentage of total nitrogen, also from the top of the canopy. Whereas removal of 20% of the total nitrogen by Rule A1 resulted in a depression of daily canopy photosynthesis by 22%, removal of 20% of the total leaf area (Rule A2) reduced daily canopy photosynthesis by 31% (Table 3, comparing photosynthesis at $K_a = 1{\cdot}3$; Fig. 3). Changes in photosynthesis shown in Fig. 3 are broadly representative of the results when the canopy top was damaged by either Rule A1 or A2.

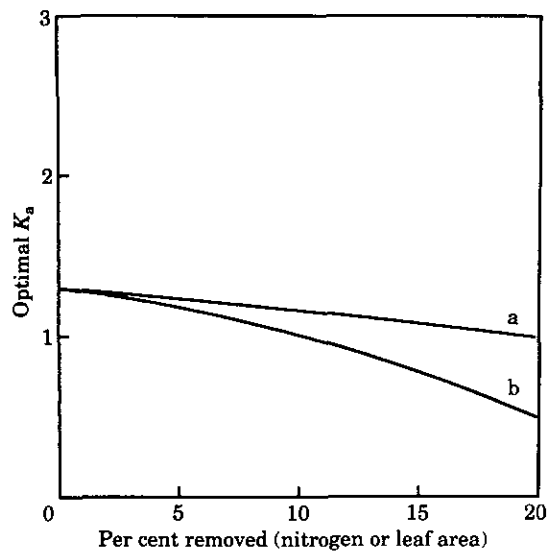

FIG. 2. Optimal nitrogen distribution (expressed as the coefficient of nitrogen allocation, K_a) as a function of severity of folivory and removal strategy (nitrogen or leaf area) when foliage is removed from the top of a canopy. Total leaf area $F_t = 4{\cdot}24$ and total canopy nitrogen $N_t = 5{\cdot}62$. (a) Rule A1: consumption of foliage with the highest nitrogen concentration first with progressive consumption of foliage of lower nitrogen concentration until the nitrogen requirement (N_R) is satisfied ($0{\cdot}01N_t \leqslant N_R \leqslant 0{\cdot}20N_t$). (b) Rule A2: consumption of foliage at the top of the canopy with progressive consumption of foliage deeper from the top until the leaf area requirement (F_R) is satisfied ($0{\cdot}01F_t \leqslant F_R \leqslant 0{\cdot}20F_t$).

3.3 HERBIVORY CAUSING AN UPWARD SHIFT IN OPTIMAL NITROGEN DISTRIBUTION

Consumption of low-nitrogen foliage (Rule B1) at the bottom of the canopy (Rule B2) resulted in an upward shift of the optimal K_a, indicating that daily canopy photosynthesis was maximized by greater concentration of nitrogen at the top than under

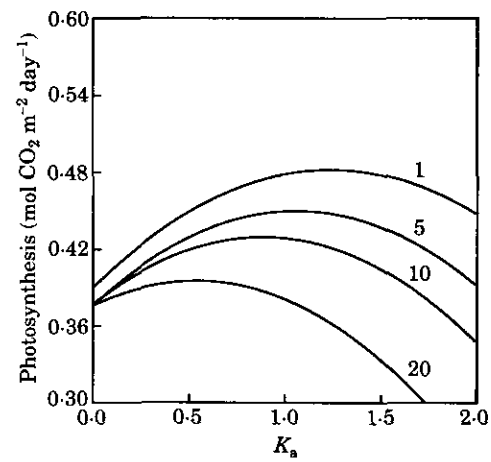

FIG. 3. Daily canopy photosynthesis as a function of nitrogen distribution pattern (coefficient of nitrogen allocation, K_a) under intensities of herbivory ranging from 1–20% leaf area removal ($0{\cdot}01F_t \leqslant F_R \leqslant 0{\cdot}20F_t$). Removal follows Rule A2: consumption of foliage at the top of the canopy with progressive consumption of foliage deeper from the top until the leaf area requirement (F_R) is satisfied. Total leaf area $F_t = 4{\cdot}24$ and total canopy nitrogen $N_t = 5{\cdot}62$.

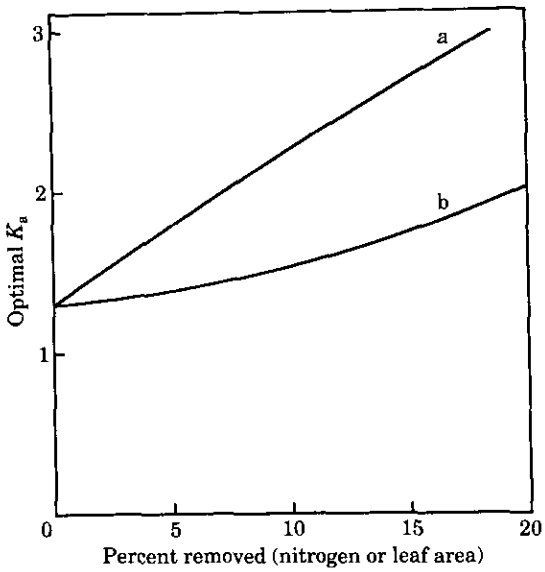

FIG. 4. *Optimal nitrogen distribution (expressed as the coefficient* of nitrogen allocation, K_a) as a function of severity of folivory and removal strategy (nitrogen or leaf area) when foliage is removed from the bottom of a canopy. Total leaf area $F_t = 4{\cdot}24$ and total canopy nitrogen $N_t = 5{\cdot}62$. (a) *Rule B1: consumption of foliage* with the lowest nitrogen concentration first with progressive consumption of foliage of higher nitrogen concentration until the nitrogen requirement (N_R) is satisfied ($0{\cdot}01N_t \leqslant N_R \leqslant 0{\cdot}20N_t$). (b) Rule B2: consumption of foliage at the bottom of the canopy with progressive consumption of foliage higher towards the top until the leaf area requirement (F_R) is satisfied ($0{\cdot}01F_t \leqslant F_R \leqslant 0{\cdot}20F_t$).

conditions of no herbivory (Table 3, Fig. 4). The upward shift resulting from consumption of low-nitrogen foliage was a much stronger response than the downward shift resulting from consumption of high-nitrogen foliage, even though identical amounts of nitrogen were consumed. Because the amount of foliage consumed had a relatively small effect on the optimal K_a (see below) when feeding occurred in the bottom of the canopy, differences in the impact of the feeding Rules A1 and B1 resulted from the position of the foliage within the canopy (top vs. bottom) rather than the different amounts of leaf area that were consumed.

In contrast to the greater effect of leaf area removal than nitrogen removal when upper leaves were consumed, the shift in K_a was greater for nitrogen removal than for leaf area removal when lower leaves were removed (Fig. 4). Under Rule B2, photosynthesis peaked at $K_a < 2{\cdot}0$ except for 20% leaf removal, whereas under Rule B1, photosynthesis peaked at $K_a > 2{\cdot}0$ for nitrogen removal of greater than 5%. This is because nitrogen is unevenly distributed, and it is the nitrogen that is photosynthetically active rather than leaves *per se*. Removal of a particular percentage of lower leaves removes less nitrogen than does removal of an identical percentage of nitrogen.

For both feeding Rules B1 and B2, the optimal K_a and therefore the optimal nitrogen concentration in the canopy top increased as the severity of herbivory increased (Fig. 5, showing Rule B2 only). At $K_a = 1{\cdot}3$, removal of 20% of the leaf area yielded virtually no change in daily canopy photosynthesis (Table 3), reflecting the smaller photosynthetic value of lower leaves.

The effect of consumption of low-nitrogen foliage on photosynthesis was negligible when K_a was low ($K_a < 1{\cdot}3$), even under fairly high levels of herbivory. At $K_a = 1{\cdot}3$, removal of 20% of the nitrogen from the bottom of the canopy yielded only a 3% reduction in photosynthesis (Table 3). When K_a was large, however ($K_a > 1{\cdot}3$), daily canopy photosynthesis was substantially higher under herbivory than when there was no herbivory (Figs 1 and 5). This seemingly paradoxical result is explained by the relationships among foliar nitrogen, gross photosynthesis, and dark respiration. Below nitrogen concentrations of $0{\cdot}66\ g\ m^{-2}$, the carbon exchange rate (net photosynthesis) becomes negative at saturating photon flux density (see P_{max}, Table 2). Hence, leaves with less nitrogen than $0{\cdot}66\ g\ m^{-2}$ represent a deficit to canopy photosynthesis at all hours of the day. Removal of these leaves by herbivores therefore removes this carbon drain, yielding an increase in net photosynthesis.

3.4. HERBIVORY CAUSING MARGINAL CHANGE IN OPTIMAL NITROGEN DISTRIBUTION

Consumption of foliage from the middle of the canopy had only a slight effect on the optimal K_a.

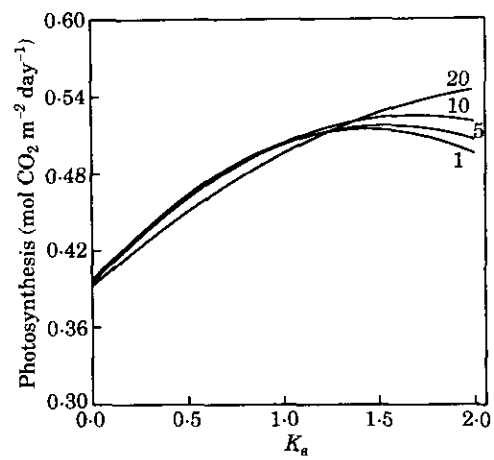

FIG. 5. Daily canopy photosynthesis as a function of nitrogen distribution pattern (coefficient of nitrogen allocation, K_a) under intensities of herbivory ranging from 1–20% leaf area removal ($0{\cdot}01F_t \leqslant F_R \leqslant 0{\cdot}20F_t$). Removal follows Rule B2: consumption of foliage at the bottom of the canopy with progressive consumption of foliage closer towards the top until the leaf area requirement (F_R) is satisfied. Total leaf area $F_t = 4{\cdot}24$ and total canopy nitrogen $N_t = 5{\cdot}62$.

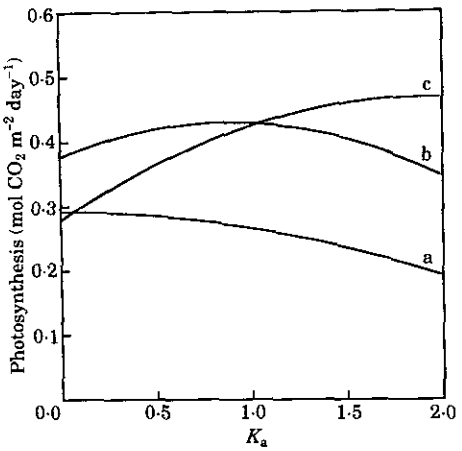

FIG. 6. Daily canopy photosynthesis as a function of nitrogen distribution pattern (coefficient of nitrogen allocation, K_a) under varying canopy densities and 10% leaf area removal. Removal follows Rule A2: consumption of foliage at the top of the canopy with progressive consumption of foliage deeper from the top until the leaf area requirement (F_R) is satisfied. Curve (a) is for $F_t = 2{\cdot}1\ m^2\ m^{-2}$, $N_t = 2{\cdot}81\ g\ m^{-2}$, curve (b) is for $F_t = 4{\cdot}24$, $N_t = 5{\cdot}62$, and curve (c) is for $F_t = 8{\cdot}48$, $N_t = 11{\cdot}24$, representing low, medium and high canopy density, respectively, where F_t = total leaf area index and N_t = total canopy nitrogen.

When herbivores removed a specific amount of nitrogen from the middle of the canopy nitrogen distribution under Rule C1, there was relatively little change in the optimal K_a under light levels of herbivory. Total canopy photosynthesis also was relatively unchanged under light levels of herbivory (1–5% of canopy nitrogen removed), and even 20% removal yielded less than a 10% reduction in the daily canopy photosynthesis when $K_a = 1{\cdot}3$ (Table 3). The difference in the change in photosynthesis for $K_a = 1{\cdot}3$ and $K_{a\,max} = 1{\cdot}0$ is slight (9·7% vs. 7·2%). When herbivores began feeding at a depth in the canopy where 30% of the total nitrogen was in higher levels, there was a greater reduction in K_a when leaf area removal was the goal than when nitrogen removal was the goal. Daily canopy photosynthesis was reduced by 10% under Rule C1, and by 14% under Rule C2 when there was 20% removal of nitrogen and leaf area, respectively (Table 3).

Effects of herbivory on optimal nitrogen distribution were even less pronounced when nitrogen or leaf area were removed beginning 30% of the total leaf area from the top of the canopy (Rules D1 and D2, respectively). When < 10% of the total leaf area was removed, the optimal K_a remained near 1·3. Greater nitrogen or leaf area removal of 20% reduced the optimal K_a to 1·1, and reduced total canopy photosynthesis by roughly 11% and 9% when $K_a = 1{\cdot}3$ and 1·1, respectively.

3.5. EFFECT OF HERBIVORY AT DIFFERENT CANOPY DENSITIES

Changes in canopy density resulted in virtually identical qualitative shifts in K_a regardless of the feeding rule applied. For example, at all canopy densities tested, removal of 10% of the leaf area at the top of the canopy caused a reduction in the optimal K_a and total photosynthesis (compare Figs 1 and 6). As canopy density increased, the optimal K_a increased by approximately the same value for all feeding rules, yielding a pattern of curves that is nearly identical for each feeding rule. This indicates that the effects of herbivory are similar in plants with different canopy densities, and that the results of the model are robust to changes in canopy density. In practical terms, this suggests that the results are not limited to plants having the particular canopy structure used in the model, but may be broadly applicable across plant species with different canopy architectures.

4. Discussion

Previous models have demonstrated the importance of crown shape and foliage distribution within crowns to plant growth (Jahnke & Lawrence, 1965; Hatch *et al.*, 1975; Kellomäki *et al.*, 1986; Kramer, 1986; Grace, 1988). Nutrient distributions among foliage appear to be of equal importance. Hirose & Werger (1987*b*) demonstrated that the distribution of canopy nitrogen that maximizes daily photosynthesis depends on the total leaf area and total nitrogen in a canopy. Because herbivory reduces both total leaf area and nitrogen in a canopy, the distribution of nitrogen that optimizes canopy photosynthesis with no herbivory may not be the same distribution that optimizes photosynthesis of a canopy damaged by herbivory. The model presented here extends that of Hirose & Werger (1987*b*) to include the effects of herbivory on optimal nitrogen distribution within a canopy. The model shows that the optimal distribution of nitrogen is a function of both the position and total surface area of leaves that are removed by herbivores.

The most striking shift in the optimal nitrogen distribution (K_a) was caused by changes in the position of foliage that was removed. When herbivory occurred in the top of the canopy [either by Rule A1 (nitrogen goal) or A2 (leaf area goal)], subsequent photosynthesis was greater in plants that had placed less nitrogen at the canopy top. Removal of leaves from the bottom of the canopy [Rules B1 (nitrogen goal) and B2 (leaf area goal)] had the opposite effect: photosynthesis following herbivory was greater in plants that had placed more nitrogen at the top of the

canopy. This suggests that plants that have different patterns of leaf loss to herbivores ideally would have evolved divergent nitrogen distribution strategies in response to expected patterns and consequences of herbivory. One may speculate that plants that are heavily browsed from the top (e.g. annuals, shrubs) should have nitrogen concentrations shifted lower in the canopy. Conversely, plants that are browsed most heavily from the bottom (e.g. tall trees) should place relatively more nitrogen towards the top of the canopy. In addition, because branches may grow out of reach of browsers as a plant grows taller (Bryant *et al.*, 1983), browsed plants may shift greater proportions of nitrogen towards the canopy top as they grow older. Plants experiencing folivory at both the canopy top and bottom would be expected to show a smaller effect of removal because of opposing effects, with the direction of the shift in nitrogen distribution depending on the relative severity of removal at the top and bottom. Insufficient data are available at this time to critically test these predictions.

It is important to note that the shifts in nitrogen distribution described above do not necessarily allow nitrogen or foliage to "escape" herbivory. This point becomes clear when comparing the effects of herbivory at the top of the canopy under different feeding rules. When total leaf removal was regulated by the amount of foliage consumed, identical amounts of foliage were removed regardless of nitrogen distribution, but plants that had their nitrogen distribution shifted away from the top lost less nitrogen. In contrast, when total leaf removal was regulated by the amount of nitrogen consumed, identical amounts of nitrogen were removed regardless of the distribution of nitrogen. However, different amounts of foliage were removed because less high-nitrogen foliage than low-nitrogen foliage was needed by herbivores in order to satisfy the nitrogen requirement. This had the interesting result that the plants that had the highest photosynthetic capacity following herbivory had more foliage removed than plants that concentrated nitrogen more towards the top.

At first analysis, plants that lose more foliage may appear to have suffered greater losses, and hence would have reduced photosynthetic capacity. However, because of the non-uniform nitrogen distribution, foliage loss does not translate directly into loss of photosynthetic capacity. To assess damage accurately, foliage position and nitrogen losses must be accounted for because loss of leaf area alone is probably a poor indicator of herbivore damage (Abrahamson & Caswell, 1982). Also, because of herbivore-related changes in canopy architecture and light penetration, photosynthetic losses cannot necessarily be calculated as a simple summation of the photosynthetic capacity of all removed foliage. What is critical to the photosynthesis of a plant following herbivory is not what resources have been *removed*, but what resources *remain*. Relative to plants with sub-optimal nitrogen distributions and photosynthetic rates, plants that had the highest photosynthetic rate following herbivory had remaining in their canopies (i) identical amounts of nitrogen distributed among fewer leaves, or (ii) more nitrogen distributed among identical leaf areas. In both cases, nitrogen content per unit area was higher when averaged across the canopy. Apparently, high photosynthetic rate following herbivory was achieved, in part, by maintaining high mean nitrogen concentrations in the foliage. The most successful plants were not those that minimized nitrogen or leaf area losses, but those that balanced these losses with respect to changes in canopy architecture and light penetration.

This has a potentially important implication with regard to plant defense. According to the nutrient stress hypothesis (Bryant *et al.*, 1983; Tuomi *et al.*, 1984), defoliation upsets the carbon/nutrient balance of a plant, and inducible changes in carbon-based allelochemicals are the result of restoring the optimal carbon/nutrient ratio. The critical importance to photosynthesis of nitrogen and its distribution suggests a corollary to this hypothesis: plants should not necessarily protect foliage *per se* (i.e. minimize loss of leaf area), but should protect the *ratio* of total nitrogen to leaf area and the distribution of nitrogen within the canopy. Inasmuch as nutrients other than nitrogen may also have optimal distributions, this reasoning applies to these as well. Rather than simply preserving some optimal carbon/nutrient ratio *in toto*, a plant also may maintain some optimal distribution of nutrients within the canopy. In some plants, increased production and mobilization of secondary plant compounds following herbivory may be a mechanism by which optimal carbon/nutrient ratios *and* nutrient distributions are restored and maintained.

The adaptive significance of plastic changes in matter partitioning in response to abiotic conditions has been discussed elsewhere (Schlichting, 1986; Bazzaz *et al.*, 1987; Chapin *et al.*, 1987). Such changes are well documented and include decreasing specific leaf weight with increasing shading (Chabot *et al.*, 1979; Fetcher *et al.*, 1983; Jurik, 1986; Oberdauer & Strain, 1986; Bongers & Popma, 1988) or with increasing leaf nitrogen concentration (Hirose, 1986, 1987), and increasing root:shoot ratio with decreasing nitrogen availability or increasing light intensity (Chapin, 1980; Hirose, 1986, 1988; Hirose & Kitajima, 1986; Hunt & Nicholls, 1986; Hara & Haraguchi, 1988).

The potential to maintain an optimal nitrogen distribution in the face of a biotic effect, herbivory, implies a similarly plastic response. Such a strategy would require mobilization and redistribution of canopy nitrogen soon after initiation of herbivore damage. The capacity for rapid response would permit optimal nitrogen distributions to be maintained both before and after herbivory, with only temporary disruption. Although direct evidence does not exist for this supposition, increased production and translocation of mobile forms of nitrogen has been reported (Baldwin, 1988*a*, *b*, 1989), and may play a dual role in plant defense and restoration of optimal nitrogen distributions.

An alternate but not mutually exclusive strategy is for a plant to have a relatively fixed response in which nitrogen is allocated in that distribution that best withstands average levels of folivory. Such plants would have sub-optimal nitrogen distributions except when the average level of folivory is incurred. Accordingly, a significant correlation is predicted between average levels of folivory and nitrogen distribution patterns. As the expected severity of damage increases, plants should take on more highly skewed or more uniform distributions than predicted when herbivory is not taken into consideration. Whether a plant responds in a fixed or plastic manner likely will depend on a variety of factors, including phylogenetic constraints (Givnish, 1987), costs associated with nutrient mobilization and redistribution (Mooney *et al.*, 1983; Chapin *et al.*, 1987), nutrient availability (Bryant *et al.*, 1983; Coley *et al.*, 1985; Hirose, 1988; Werger & Hirose, 1988) and the expected incidence of folivory over the lifetime of a plant.

Finally, the increase in daily canopy photosynthesis found after removal of low-nitrogen foliage (Rules B1, B2) would appear to raise anew the possibility that herbivory may actually enhance the fitness of a plant. This possibility has been suggested previously for a variety of reasons, but has largely been discounted (see Belsky, 1986). Although this model defines conditions under which herbivory could cause an increase in photosynthesis, several considerations suggest that these conditions would rarely be met, and that herbivory is *not* likely to enhance plant fitness. First, foliage with low nitrogen concentrations ($<0{\cdot}66\,g\,m^{-2}$) is probably rare. The observed minimum nitrogen concentration of living *Solidago altissima* leaves is about $0{\cdot}90 \pm 0{\cdot}08\,g\,m^{-2}$ (mean ± S.D.), and dead leaves are approximately $0{\cdot}44 \pm 0{\cdot}06\,g\,m^{-2}$ (Hirose & Werger, 1987*b*). Presumably, plants will not maintain leaves at very low N concentrations if they pose a deficit to canopy photosynthesis (Mooney & Gulmon, 1982). However, all leaves on a plant are likely to pass through this range of nitrogen levels as they senesce. Second, much of the nitrogen in a senescing leaf will be translocated to other parts of the plant, possibly to new foliage at the top of the canopy. Removal of nitrogen by herbivores thus has a lost opportunity cost that is not estimated by the model. Third, optimization of nitrogen distribution is possible not only within a canopy, but within individual leaves as well (Evans, 1989). Acclimation to low irradiance may result in a partitioning of nitrogen within a leaf among RuBP carboxylase and thylakoid nitrogen that differs from that of leaves growing under high irradiance. This may alter the balance of gross photosynthesis and dark respiration so that lower leaves have higher (or lower) net photosynthesis and deficit threshold than assumed. Fourth, plant fitness is a function of more than just canopy photosynthesis, although canopy photosynthesis may be a major component. This model focuses exclusively on effects on canopy photosynthesis and does not make direct predictions regarding plant fitness.

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APPENDIX—*overleaf*

APPENDIX A

Symbol Definitions

N_L	Nitrogen concentration per unit leaf area; $g\,m^{-2}$
N_0	N_L at the top layer of the canopy; $g\,m^{-2}$
K_a	Coefficient of nitrogen allocation; dimensionless
F	Leaf area index from the canopy top; $m^2\,m^{-2}$
F_t	Total leaf area per unit ground area; $m^2\,m^{-2}$
N_t	Total leaf nitrogen per unit ground area; $g\,m^{-2}$
N_R	Nitrogen removed by herbivores; $g\,m^{-2}$
L_R	Leaf area removed by herbivores; $m^2\,m^{-2}$
I_t	Irradiance on a leaf surface; $\mu E\,m^{-2}\,sec^{-1}$
I_0	Irradiance on a horizontal plane above the canopy; $\mu E\,m^{-2}\,sec^{-1}$
$\hat{I}$	I_0 at 1200 hr; $\mu E\,m^{-2}\,sec^{-1}$
K_t	Coefficient of light extinction; dimensionless
m	Transmission coefficient of light; dimensionless
t	Solar time; hr
P	Net photosynthesis (instantaneous CO_2 exchange rate of an individual leaf; $\mu mol\ (CO_2)\ m^{-2}\,sec^{-1}$
P_{day}	Daily canopy (net) photosynthesis (CO_2 exchange rate); $mol\ (CO_2)\ m^{-2}\,day^{-1}$
P_g	Gross photosynthesis (P plus dark respiration) of an individual leaf; $\mu mol\ (CO_2)\ m^{-2}\,sec^{-1}$
P_{max}	Gross photosynthesis at light saturation; $\mu mol\ (CO_2)\ m^{-2}\,sec^{-1}$
R	Dark respiration; $\mu mol\ (CO_2)\ m^{-2}\,sec^{-1}$
a_m	Y intercept in the regression of P_{max} vs. N_L; $\mu mol\ (CO_2)\ m^{-2}\,sec^{-1}$
a_p	Y intercept in the regression of ϕ vs. N_L; $\mu mol\ (CO_2)\ \mu E^{-1}$
a_r	Y intercept in the regression of R vs. N_L; $\mu mol\ (CO_2)\ m^{-2}\,sec^{-1}$
a_t	Y intercept in the regression of $\ominus$ vs. N_L; dimensionless
b_m	Slope in the regression of P_{max} vs. N_L; $\mu mol\ (CO_2)\ m^{-2}\,sec^{-1}$
b_p	Slope in the regression of ϕ vs. N_L; $m^{-2}\,g^{-1}$ (N)
b_r	Slope in the regression of R vs. N_L;
b_t	Slope in the regression of $\ominus$ vs. N_L; $\mu mol\ (C)_2\ g^{-1}$ (N) sec^{-1}
ϕ	Quantum yield (initial slope of a light response curve of photosynthesis); $\mu mol\ (CO_2)\ \mu E^{-1}$
$\ominus$	Convexity of a light response curve of photosynthesis; dimensionless

APPENDIX B

The light response of net photosynthesis is described by regressions with N_L as

$$R = a_r + b_r N_L$$
$$P_{max} = a_m + b_m N_L$$
$$\phi = a_p + b_p N_L$$
$$\ominus = a_t + b_t N_L,$$

where a_i and b_i are regression coefficients.