

# Optimality and nitrogen allocation in a tree canopy

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**Summary** Physical and functional properties of foliage were measured at a variety of microsites in a broad-leaved *Nothofagus fusca* (Hook. f.) Ørst. canopy. The light climate of the foliage at these sites was monitored for 39 days in the late spring and early summer with *in situ* sensors. Foliage nitrogen content (N), mean leaf angle, and gas exchange characteristics were all correlated with the amount of light reaching the microsites during foliage development. Foliage N content on a leaf area basis ranged between  $\sim 1$  and  $2.5 \text{ g N m}^{-2}$  and was highest at the brightest sites. Light-saturated photosynthetic rates ranged between  $\sim 4$  and  $9 \mu\text{mol m}^{-2} \text{ s}^{-1}$ , increasing from the darkest to brightest sites.

A biochemical model of photosynthesis was fitted to foliage characteristics at the different microsites and used to integrate foliage assimilation among the sites over 39 days. The actual arrangement of foliage physiological characteristics in the observed microsites led to higher total canopy rates of net assimilation than >99% of the combinations of observed foliage characteristics randomly assigned to the observed microsites. Additional simulations first related the maximum rates of electron transport ( $J_{\text{max}}$ ), ribulose biphosphate turnover ( $V_{\text{c,max}}$ ), and dark respiration ( $R_d$ ) of *Nothofagus fusca* foliage to nitrogen content and then allowed foliage N (and consequently leaf gas exchange characteristics) to vary across the canopy. The observed N allocation pattern results in greater total canopy assimilation than uniform or >99% of the simulations with random distributions of N among the microsites (constrained so that the total N allocated was equivalent to that observed in the microsites). However, the observed pattern of N allocation places less N in the brightest microsites and results in substantially less total assimilation than a simulated canopy in which N was allocated in an optimal manner where the N distribution is such that the partial derivative of leaf assimilation ( $A$ ) with respect to leaf nitrogen content,  $\partial A / \partial N$ , is constant among microsites. These results suggest that other factors such as wind or herbivory reduce the integrated assimilation of high-N foliage relatively more than lower-N foliage and that a  $\partial A / \partial N$  optimality criteria based only on formulations of leaf gas exchange overestimate canopy assimilation.

**Keywords:** light penetration, optimization, photosynthesis model, remote sensing, simulation model.

## Introduction

The positive relationship between leaf nitrogen and photosynthetic capacity (e.g., Mooney and Gulmon 1979, Field 1983, Field and Mooney 1986) is one of the most robust results of modern ecophysiology. This relationship is based on the fact that the principal carboxylating enzyme of plants, ribulose-bisphosphate carboxylase-oxygenase (Rubisco) makes up a significant fraction of the total leaf protein (Björkman 1968). Because nitrogen is generally a scarce resource that limits plant carbon gain (Chapin et al. 1987), natural selection will favor individuals that allocate N in an efficient manner through the canopy (Field 1983, Hirose and Werger 1987, Hollinger 1989, Field 1991). Field (1983) suggested that N would be allocated optimally in a plant canopy when the marginal increase in assimilation ( $A$ ) with an increase in N was constant throughout the canopy ( $\partial A / \partial N$  constant). Studies of N allocation in a variety of tree and crop species indicating that more N is allocated per unit foliage area or per unit foliage mass in the brighter sites at the top of a canopy than at the darker sites lower in the canopy are consistent with this hypothesis (e.g., Field 1983, DeJong and Doyle 1985, Hirose and Werger 1987, Hirose et al. 1989, Hollinger 1989, Evans 1989, Leuning et al. 1991a, 1991b, Ellsworth and Reich 1993). Several studies (Sellers et al. 1992, Wu 1993, Anten et al. 1995) have addressed this issue analytically for simple radiation models in one-dimensional plant canopies and shown that  $\partial A / \partial N$  is constant when N is allocated at a site within the canopy in proportion to the fraction of photosynthetically active radiation (FPAR, hereafter referred to as the fraction of photosynthetically active photon flux density,  $F_{\text{PPFD}}$ ) received at that site. Field validation of these results is desirable because the results of Sellers et al. (1992) provide important simplifications and constraints for models of land surface  $\text{CO}_2$  exchange.

The goal of this study was to assess the optimal allocation hypothesis experimentally with coordinated measurements of light, N, and photosynthetic performance in a variety of microsites in the canopy of a large forest tree species. A model that coupled stomatal conductance to assimilation was used to integrate assimilation over time and among microsites based on the half-hourly mean photosynthetically active photon flux density (PPFD) in each microsite and above-canopy values for temperature and humidity. In the first set of simulations, leaf parameters were estimated for foliage in each microsite. This

allowed the calculation of canopy assimilation with leaves in their native positions to be compared with simulations in which leaves were substituted into other than their original PPFD microsites. In a second set of simulations, key leaf parameters were related to leaf nitrogen values and the N at any microsite used to set model parameters for subsequent simulations. This allowed the calculation of canopy assimilation with the observed pattern of N distribution to be compared with other ways of allocating the same total quantity of N among the microsites.

## Materials and methods

This study was carried out in undisturbed, old-growth *Nothofagus* forest near the township of Maruia, South Island, New Zealand (42°12' S, 172°15' E; 400 m a.s.l.). The forest is dominated by emergent *Nothofagus fusca* (Hook. f.) Ørst. (red beech) trees, a temperate, broad-leaved evergreen, approximately 30 m tall with a 15-m canopy depth. The vegetation, soils, climate, and forest-atmosphere gas and energy exchange at this site have been described elsewhere (Stewart et al. 1991, Kelliher et al. 1992, Hollinger et al. 1994).

The canopy was reached with a 32-m tall square scaffolding tower. A column of canopy ~9 m on a side was accessible from the tower. Microsites within the canopies of several *Nothofagus fusca* were chosen to represent the range of light conditions from the top (~32 m) to the lowest layers at ~17 m. Photodiodes (NEC model PH-201A) were affixed to horizontal supports at 30 of these microsites, and the photosynthetically active photon flux densities (PPFD) recorded at 3-s intervals and stored as 30-min averages with a system consisting of Model 21X data logger and two model AIM16 multiplexers (Campbell Scientific, Logan, UT). The lack of near infrared sensitivity in the photodiodes makes them suitable PPFD sensors within the canopy (Gutschick et al. 1985). Data were recorded for 39 days, starting in the southern spring just before leaf expansion (Julian Day 302) and finishing about 4 weeks after new leaves were fully expanded. Total and diffuse PPFD, rainfall, wind speed, wind direction, air temperature, and relative humidity were measured above the canopy.

The foliage of branches at the microsites was sampled in early summer to determine leaf size, mass, nitrogen concentration, and orientation. These data were used to calculate the foliage mass per unit area, N content per unit area, and G-function for leaf radiation interception (Lemur 1973, Ross 1981). Canopy sampling methodology and sample preparation followed Hollinger (1989). Neutral density shade cloth bags (~50% shade) were affixed to eight branches before bud break to determine if leaf N content was affected by PPFD exposure during leaf expansion. Control and shaded foliage N contents were compared with a paired *t*-test.

Leaf gas exchange characteristics were determined during the (southern) summer of 1990 at 14 of the PPFD microsites and several other locations in the canopy with the system consisting of two climatized cuvettes described in Hollinger (1987). Cuvette CO<sub>2</sub> partial pressure was regulated by mixing CO<sub>2</sub>-free air with ~1% CO<sub>2</sub> in N<sub>2</sub> by mass flow controllers (Tylan Corp., Torrance, CA). At each site, water vapor and CO<sub>2</sub>

exchange were measured at three different partial pressures of CO<sub>2</sub> (~150, 300, and 450 μmol CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup>; ~1000 μmol m<sup>-2</sup> s<sup>-1</sup> PPFD) and at a range of PPFDs (~340 μmol CO<sub>2</sub> mol<sup>-1</sup>). The influences of temperature and leaf-air vapor pressure difference ( $\Delta W$ ) on leaf gas exchange were determined on an additional four samples of foliage. All gas exchange data were calculated using the equations of Farquhar and Sharkey (1982) and expressed on a projected area basis.

## Leaf model

Gas exchange data were used to estimate the biochemical parameters of a mechanistic model of leaf assimilation described by Berry and Farquhar (1978) and further developed by Farquhar et al. (1980) and Farquhar and von Caemmerer (1982). The model of leaf assimilation was coupled to a semi-empirical model of stomatal conductance (Ball et al. 1987, Ball 1988) following generally after Collatz et al. (1991) and Leuning (1995). The coupled models were used to estimate integrated daily assimilation within and between the different microsites of the *Nothofagus* canopy based on the measured PPFD data at each microsite. In this way the performance of foliage that developed in one microsite could be evaluated in other microsites.

Following Farquhar and von Caemmerer (1982), assimilation (*A*) is calculated as;

$$A = V_c(1 - \Gamma^*/C_i) - R_d, \quad (1)$$

where  $V_c$  is the carboxylation velocity,  $\Gamma^*$  is the CO<sub>2</sub> compensation point without dark respiration,  $C_i$  is the intercellular partial pressure of CO<sub>2</sub>, and  $R_d$  is the rate of dark respiration. The carboxylation velocity is the lesser of either the ribulose biphosphate (RuP<sub>2</sub>) saturated rate ( $W_c$ ) or the electron transport limited rate of RuP<sub>2</sub> regeneration ( $J'$ ) (Farquhar et al. 1980). The RuP<sub>2</sub> saturated rate is regulated by a maximum carboxylation velocity ( $V_{c,max}$ ),  $C_i$  is the intercellular partial pressure of O<sub>2</sub> ( $O_i$ ), and the Michaelis constants for CO<sub>2</sub> ( $K_c$ ) and O<sub>2</sub> ( $K_o$ ).

The maximum rate of electron transport depends on irradiance ( $I$ ) and a maximum rate of electron transport ( $J_{max}$ ) (Farquhar and von Caemmerer 1982).

Because enzymatic reaction rates are temperature dependent, the Michaelis constants, dark respiration rate and maximum rate of RuP<sub>2</sub> turnover are adjusted with the Arrhenius relation so that the rate at temperature  $T$  (rate<sub>*T*</sub>) is based on the rate at a base temperature (rate<sub>20</sub>) as;

$$\text{rate}_T = \text{rate}_{20} e^{((T_K - 293.16)E/(293.16 RT_K))}, \quad (2)$$

where  $T_K$  is the absolute temperature,  $E$  is the activation energy (Table 1), and  $R$  is the universal gas constant (8.314 J K<sup>-1</sup> mol<sup>-1</sup>). For the temperature response of  $J_{max}$ , Farquhar et al. (1980) used a simplified version of an equation developed by Sharpe and DeMichelle (1977) that describes the effect of temperature on enzyme inactivation.

Activation energies were determined by back-fitting the model using non-linear least squares fits to the assimila-

Table 1. Symbols, units, values and definitions for *Nothofagus fusca* leaf assimilation and stomatal conductance models (temperature-dependent parameters as at 20 °C).

| Symbol                                               | Value   | Definition                                                                         |
|------------------------------------------------------|---------|------------------------------------------------------------------------------------|
| $C_i$ (Pa)                                           | 24.5    | Intercellular partial pressure of CO <sub>2</sub> (varies with $I$ , $g_s$ , etc.) |
| $O$ (Pa)                                             | 21,000  | Partial pressure of O <sub>2</sub>                                                 |
| $\Gamma^*$ (Pa)                                      | 3.1     | CO <sub>2</sub> compensation point without $R_d$                                   |
| $V_{c,max}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) | 40      | Maximum carboxylation velocity (varies with leaf N)                                |
| $J_{max}$ ( $\mu\text{Eq m}^{-2} \text{s}^{-1}$ )    | 80      | Light saturated rate of electron transport (varies with leaf N)                    |
| $K_c$ (Pa)                                           | 41      | Michaelis constant for CO <sub>2</sub>                                             |
| $K_o$ (Pa)                                           | 35,000  | Michaelis constant for O <sub>2</sub>                                              |
| $S$ ( $\text{J K}^{-1} \text{mol}^{-1}$ )            | 700     | Temperature coefficient for $J_{max}$                                              |
| $H$ ( $\text{J mol}^{-1}$ )                          | 209,200 | Temperature coefficient for $J_{max}$                                              |
| $f$                                                  | 0.13    | Fraction of light not absorbed by chloroplasts                                     |
| $m$                                                  | 9.4     | Slope factor of conductance                                                        |
| $b$ ( $\text{mol m}^{-2} \text{s}^{-1}$ )            | 0.15    | Stomatal conductance intercept                                                     |
| Activation energy ( $\text{J mol}^{-1}$ ) values     |         |                                                                                    |
| $K_c$                                                | 68,400  |                                                                                    |
| $K_o$                                                | 33,950  |                                                                                    |
| $R_d$                                                | 56,400  |                                                                                    |
| $V_{c,max}$                                          | 47,500  |                                                                                    |
| $J_{max}$                                            | 37,000  |                                                                                    |

tion/temperature curves and Michaelis coefficients were estimated similarly from  $A/C_i$  curves following the methods of Kirschbaum and Farquhar (1984) and Brooks and Farquhar (1985). The activation energies and Michaelis coefficients were equivalent for all leaves in the simulations. Individual values for  $J_{max}$  and  $V_{c,max}$  were then determined for foliage in the 14 microsites based on back-fitting the model using non-linear least square fits to  $A/C_i$  and  $A/PPFD$  curves from each microsite. The internal values of CO<sub>2</sub> used in these fits were the values calculated from the gas exchange measurements of CO<sub>2</sub> and H<sub>2</sub>O exchange.

Stomatal conductance ( $g_s$ ) was calculated based on the semi-empirical relationship of Ball et al. (1987) as modified by Ball (1988);

$$g_s = m A h_s / C_s + b, \quad (3)$$

where  $h_s$  is the relative humidity and  $C_s$  is the CO<sub>2</sub> mole fraction (both at the leaf surface) and  $m$  and  $b$  are the slope and intercept obtained from regression analysis of cuvette gas exchange measurements. These coefficients were fitted from the total data set of *Nothofagus* CO<sub>2</sub> and H<sub>2</sub>O exchange measurements (all  $A/C_i$ ,  $A/\Delta W$  and  $A/PPFD$  curves where the PPFD was  $> 20 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Aphalo and Jarvis (1993) and Leuning (1995) present alternative, more mechanistic formulations of this relationship, but for the present study, Equation 3 was found sufficient.

The total assimilation of foliage in 14 microsites was determined by running the coupled assimilation-conductance model for 39 days at a 30-min time step with the PPFD data for each microsite and above-canopy values of  $T$  and RH. The values of  $V_{c,max}$ ,  $J_{max}$  and  $R_d$  of foliage in each microsite were determined from the gas exchange measurements. All other

model parameters were identical among microsites. The external concentration of CO<sub>2</sub> was fixed at  $340 \mu\text{l l}^{-1}$ . The integrated assimilation of leaves in their observed microsites was then compared with 5000 integrations of assimilation for foliage of the observed characteristics randomly assigned to the 14 microsites. In these simulations, the set of  $V_{c,max}$ ,  $J_{max}$  and  $R_d$  measured for each microsite was randomly assigned to a microsite such that each set was used once and assimilation summed for all sites over the 39 days.

In a second set of simulations, the total assimilation of foliage in the 14 microsites over 39 days was calculated as a function of foliage N content. To do this,  $V_{c,max}$ ,  $J_{max}$  and  $R_{d20}$  were related to foliage N content by linear regression (Field 1983, Harley et al. 1992, Hollinger 1992). In the simulations here, the amount of N in each microsite was allowed to vary continuously within a range set by 80% of the lowest and 120% of the highest observed N content values. The total N content allocated among the 14 microsites was constrained to the observed total,  $26.09 \text{ g m}^{-2}$ . Additional simulations were carried out with the actual N allocation pattern, N allocated equally to the 14 sites, and to determine constrained (leaf N limited to the range of values observed in the field) and unconstrained (no limit to leaf N content except overall canopy limit of  $26.09 \text{ g N m}^{-2}$ ) patterns of N allocation that maximized total C gain over the 39-day sample period.

## Results

### Canopy light environment

On sunny days, the maximum half-hourly PPFD at this southern hemisphere site exceeded  $2200 \mu\text{mol m}^{-2} \text{s}^{-1}$ . However, on 13% of the study days the maximum above-canopy PPFD never exceeded  $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Integrated daily above-

canopy PPFD ranged between 12 and 70 mol m<sup>-2</sup>. Overcast or predominantly diffuse light conditions were more common during foliage development than clear skies. During about 64% of the 30-min time periods within 4 h of solar noon, total PPFD was two-thirds or more diffuse. By contrast, during only 21% of these time periods did direct beam radiation exceed two-thirds or more of the total PPFD.

Sampled foliage microsites received photosynthetically active photon flux densities that ranged from 100 to about 8% of the above-canopy values. Examination of the fraction of total PPFD that was received at each sensor under clear (< 30% above-canopy diffuse PPFD) versus overcast conditions (> 70% above-canopy diffuse PPFD), shows that a higher proportion of above-canopy diffuse radiation penetrates through the canopy than direct beam radiation (Figure 1), presumably because of a higher frequency of gaps overhead than in the path of the solar beam.

#### Leaf morphological characteristics

Leaf size, angle, and leaf mass per unit area (LMA) all varied significantly as a function of microsite light environment (Figure 2). Leaves in the brighter microsites were about half the size of those in the darkest sites but had twofold higher LMA, indicating that individual leaf mass was roughly constant. Leaf nitrogen concentration did not vary significantly among leaves in the different microsites (data not shown), but because of the strong gradient in LMA, nitrogen mass per unit area (NMA) also varied among microsites (Figure 3). The variation in N was directly related to foliage PPFD during foliage development; the NMA of foliage from bright microsites that was shaded with neutral density screening was significantly less than that of adjacent, unshaded foliage ( $t = 4.56$ ,  $P < 0.01$ ), and more similar to foliage from lower PPFD microsites (Figure 3).

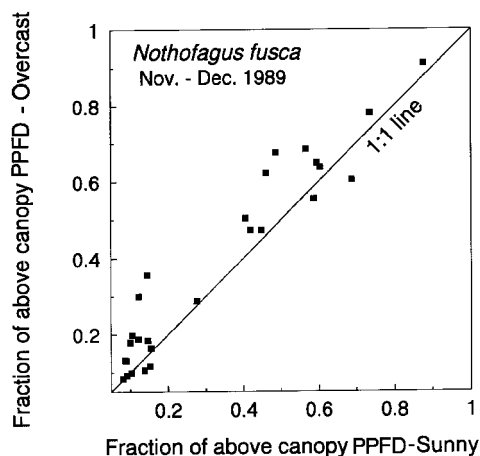


Figure 1. Fraction of above-canopy PPFD reaching the fixed sensors during clear (diffuse PPFD < 30% of total) and overcast (diffuse PPFD > 70% of total) conditions. The PPFD fractional penetration is significantly greater under overcast than clear conditions ( $P < 0.01$ ,  $z$  test).

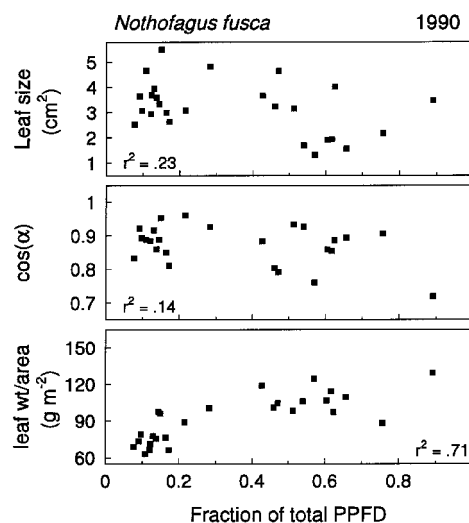


Figure 2. Foliage characteristics as a function of the foliage PPFD environment.

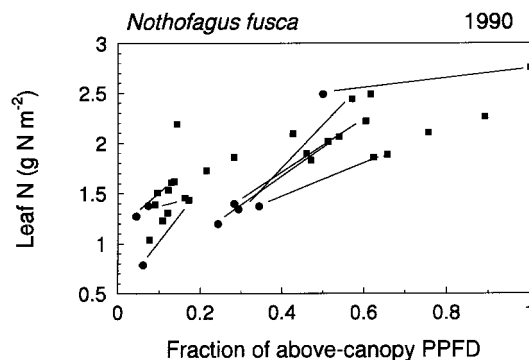


Figure 3. Foliage nitrogen mass per unit area as a function of the foliage light environment. The lines connect control foliage samples with adjacent samples shaded with neutral density shade cloth.

#### Leaf physiological properties

Light saturated photosynthesis ( $A_{\max}$ ) and dark respiration at 20 °C ( $R_d$ ) both varied significantly ( $P < 0.05$ ) as a function of the foliage microsite light environment (Figure 4). For  $A_{\max}$  and  $R_d$ , rates at the bottom of the canopy were about one-half and one-third, respectively, of those at the top. For  $A_{\max}$ , the pattern of the residuals suggest that a saturating or curvilinear relationship may be a better model than the linear relationship shown in Figure 4.

The temperature optimum for *Nothofagus* assimilation was about 18 °C and dropped off rapidly above about 23 °C (Figure 5). This response is consistent with the moderate summer temperatures at the site (Hollinger et al. 1994). The temperature response was simulated in the model by fitting the activation energies and  $H$  and  $S$  in the  $J_{\max}$  relationship (Table 1 and Figure 5).

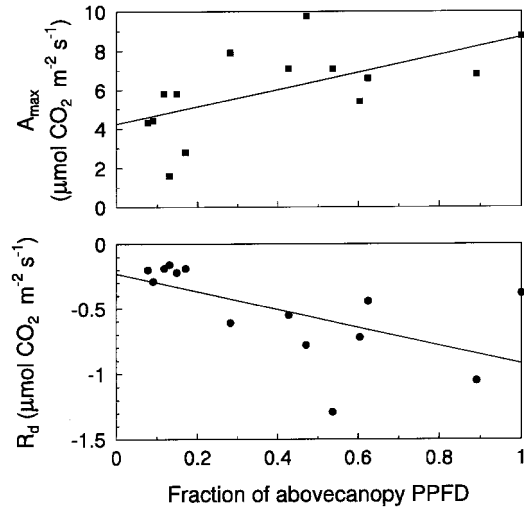


Figure 4. Leaf saturated photosynthesis,  $A_{\max}$ , (PPFD = 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and dark respiration,  $R_d$ , at 20 °C as a function of the foliage microsite light environment. Solid lines are linear regressions between the fraction of above-canopy PPFD,  $F_{\text{PPFD}}$ , and  $A_{\max}$  ( $A_{\max} = 4.2 + 4.5F_{\text{PPFD}}$ ,  $r^2 = 0.37$ ,  $P < 0.05$ ) and  $F_{\text{PPFD}}$  and  $R_d$  ( $R_d = -0.2 - 0.7F_{\text{PPFD}}$ ,  $r^2 = 0.36$ ,  $P < 0.05$ ).

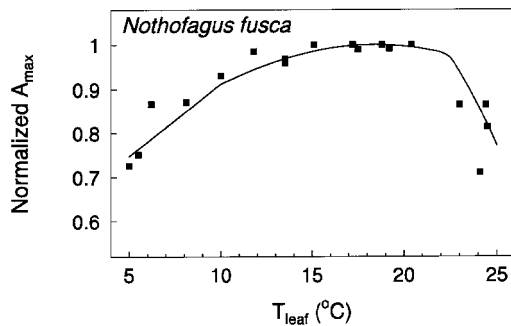


Figure 5. *Nothofagus* leaf assimilation as a function of temperature (leaf–air vapor pressure difference < 1 kPa). The solid line is the modeled response.

The slope and intercept from a plot of  $Ah_s/C_s$  versus  $g_s$  (Figure 6) for *Nothofagus* were about 9.4 and 0.15  $\text{mol } \mu\text{m}^{-2} \text{s}^{-1}$ , respectively, which are values similar to those used by Collatz et al. (1991). Because of the uniformity of this relationship, constant values for the slope and intercept were used for all leaves in the simulation studies.

#### Canopy assimilation

Simulated total assimilation of leaves in their native microsites was greater than for more than 99.5% of the simulated arrangements of leaves randomly assigned to microsites (Figure 7A). The total assimilation was > 98% of the maximum possible by any combination of the observed foliage in the microsites. Given the inevitability of error in both the light environment and foliage gas exchange measurements, the actual arrangement of leaves in microsites is probably indistinguishable from

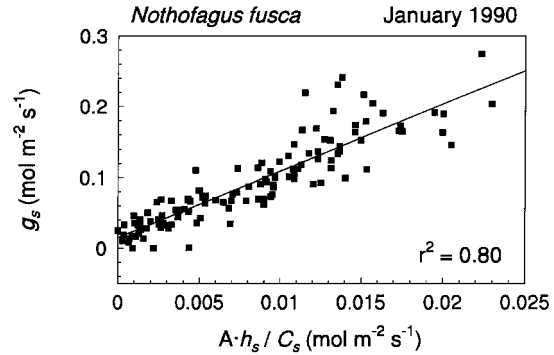


Figure 6. *Nothofagus* stomatal conductance data plotted against  $Ah_s/C_s$ .

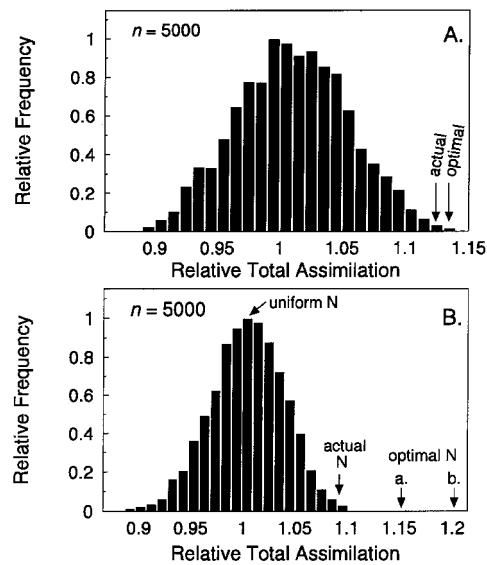


Figure 7. A. Relative integrated assimilation of 5000 canopies composed of leaves with observed physiological characteristics randomly assigned to the 14 microsites compared to the performance of the observed leaves in their observed microsites. B. Relative integrated assimilation of 5000 canopies composed of leaves with variable N content (but equivalent total quantity) randomly assigned to 14 microsites compared with the performance of canopies with: (i) the actual N arrangement; (ii) a uniform (equal) distribution of N; and (iii) the optimum allocation of N (a. = with each leaf constrained to the range of N observed, and b. = the unconstrained optimal allocation of N). ( $V_{c,\max} = 2.26 + 14N$ ,  $J_{\max} = 7.35 + 37N$ , and  $R_d = -0.17 + 0.36N$ , where N is leaf nitrogen content in  $\text{g m}^{-2}$ .)

the optimum arrangement of the observed leaves in the canopy sites.

When the broader problem of leaves of any N content is considered, however, the results are less clear (Figure 7B). The actual allocation of N in leaves in the microsites results in simulated integrated carbon gain that is greater than that from more than 99.5% of all trials where N is randomly allocated among the microsites (constrained to be > 80 and < 120% of the observed minimum and maximum leaf N contents). The total amount of assimilate produced with the actual pattern of

N allocation is about 8.5% greater than the mean of simulations in which N is randomly allocated and about 6.5% greater than allocating an equal amount of N to all microsites.

However, the simulated integrated canopy carbon gain for the observed canopy is about 5.5% less than that of a canopy where the total N is equivalent to that observed in the field and the N per leaf is allowed to vary across the observed range of values but allocated optimally (Figures 7B and 8). Removing the constraint that leaf N contents are limited to values observed in the field allows the unconstrained allocation pattern where  $\partial A/\partial N$  is equivalent throughout the canopy. This produces the allocation pattern where N content is approximately proportional to the fraction of PPFD received at each microsite (Figure 8). Canopy assimilation for this case is about 11% greater than for the observed canopy (Figure 7B). The simulated carbon gain of the observed canopy is thus about midway between canopies in which a fixed amount of N is allocated equally among all leaves or allocated so that  $\partial A/\partial N$  is the same for all leaves.

## Discussion

This and other studies (e.g., DeJong and Doyle 1985, Hollinger 1989, Vapaavuori and Vuorinen 1989, Leuning et al. 1991a, Ellsworth and Reich 1993) demonstrate that N is not allocated randomly within tree canopies. Simulations show that the observed patterns of N allocation result in a greater canopy carbon gain than patterns in which the same total quantity of N is allocated randomly or equally among microsites.

The present results, however, do not support the hypothesis that the distribution of canopy N maximizes instantaneous (or integrated) assimilation. There was less N in the brighter sites and more in the darker sites than is optimal according to the  $\partial A/\partial N$  criterion. Similar results have recently been obtained from studies with herbaceous species (Evans 1993, Anten et al. 1995). There is undoubtedly a limit to allocation flexibility; tree canopies do not have a perfect ability to sense and compare light environments in different microsites and to translocate N accordingly. This is particularly true once a canopy has devel-

oped (but see Evans 1993). The shading experiments (Figure 3), however, support a high degree of allocation flexibility, at least during leaf expansion.

A more likely reason why the canopy pattern of N allocation deviates from the  $\partial A/\partial N$  optimality prediction is that the carbon "cost" to nitrogen in this formulation is implicitly either zero or scales linearly with N. A better optimality criterion would be to take N costs into account and calculate net assimilation after costs,  $\partial A/\partial N - \partial C/\partial N$ , where  $\partial C/\partial N$  is the partial derivative of the carbon cost with respect to N (Mooney and Gulmon 1979). These costs include the direct carbon costs of leaf construction and dark respiration as well as indirect costs associated with nutrient uptake and possible increased leaf losses with higher N. Mooney and Gulmon (1979) discuss the possibility of leaf herbivory increasing with higher leaf N and argue that leaf costs increase more than linearly with N. Under this alternate optimality criterion, any factors other than PPFD that affect leaf carbon gain or loss differently at different locations in the canopy will also influence the optimal distribution of N. This means factors such as sunflecks, photoinhibition, and wind can have an effect similar to herbivory. For example, photoinhibition might reduce the assimilation of treetop foliage, and higher windspeeds may increase the probability of loss of exposed leaves. The foliage most exposed to photoinhibition and wind is that with the most N at the top of the canopy, suggesting increased costs for high-N (exposed) leaves. In this instance, maximizing canopy photosynthesis by keeping  $\partial A/\partial N - \partial C/\partial N$  constant would require less N in the most exposed sites (and more elsewhere) than the  $\partial A/\partial N$  criterion. Thus, the result of including costs associated with both leaf properties and physical location is to reduce the slope of the relationship between  $F_{PPFD}$  and leaf N, consistent with observation (Figure 8).

## Conclusions

The pattern of N allocation in a canopy must be determined to model assimilation at the scale of the canopy, stand, or landscape effectively. The first generation of canopy models (e.g., de Wit 1965, Duncan 1971) assumed a uniform distribution of N which may *underestimate* canopy assimilation by 5–10% if based on assimilation of foliage with an average N content. Sellers et al. (1992) used the rationale of optimizing canopy assimilation to propose a pattern where canopy N varied so that leaf N content was proportional to the fraction of above-canopy PPFD reaching the foliage. The present study and other recent work (Evans 1993, Anten et al. 1995) suggest that this allocation pattern *overestimates* canopy assimilation by 5–10%. A better accounting of the costs associated with the acquisition of N and construction of the assimilatory system should lead to improved models of canopy N allocation. Because a number of independent factors affect costs, such an analysis will be more difficult than that of determining the relationship between N and A.

In the meantime, modelers may wish to follow the pragmatic approach and allocate N as a linear function of the microsite PPFD:

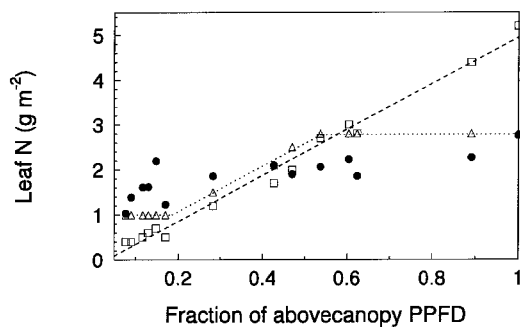


Figure 8. Relationship between microsite fraction of above-canopy PPFD and N allocation for the observed canopy (circles), for an optimal distribution of N when leaf N is constrained to the range of values observed in the field (triangles and dotted line), and for an optimal distribution of N ( $\partial A/\partial N$  constant) without constraints on individual leaf values (squares and dashed line).

$$N = F_{\text{PPFD}}(N_{\text{max}} - N_{\text{min}}) + N_{\text{min}}, \quad (4)$$

where  $N$  is the nitrogen mass per unit foliage area at any location in the canopy,  $F_{\text{PPFD}}$  is the fraction of the above-canopy PPFD striking the foliage,  $N_{\text{max}}$  is the maximum (top of canopy) N mass per unit foliage area and  $N_{\text{min}}$  is the minimum (bottom of canopy) N mass per unit foliage area. For tree canopies with moderate to high LAI, present data (Hollinger 1989, Ellsworth and Reich 1993, this study) suggest about a 2.5-fold range between  $N_{\text{min}}$  and  $N_{\text{max}}$ .

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