

# Optimal co-allocation of carbon and nitrogen in a forest stand at steady state

## Supplemental material

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### Solution of the optimisation problem

At steady state,  $W_f$ ,  $W_r$ , and  $W_w$  are constant, so we can write  $W_r = \phi_r W_f$ , and from (Eqn 12) and (Eqn 16),  $W_w = \alpha_w c_H [N]_f W_f$ . Consequently, under the assumptions of the model, the production rate of total biomass at steady state is

$$G = \frac{W_f}{T_f} + \frac{W_r}{T_r} + \frac{W_w}{T_w} = W_f \left( \frac{1}{T_f} + \frac{\phi_r}{T_r} + \frac{\alpha_w c_H [N]_f}{T_w} \right). \quad \text{Eqn S1}$$

Hence, from (Eqn 4),

$$W_f \left( \frac{1}{T_f} + \frac{\phi_r}{T_r} + \frac{\alpha_w c_H [N]_f}{T_w} \right) = Y (P - R_m). \quad \text{Eqn S2}$$

Substituting our expressions for  $R_m$  and  $P$  from (Eqn 5) and (Eqn 6), respectively, we obtain steady state  $W_f$  from the carbon balance as a function of  $\phi_r$  and  $[N]_f$ , i.e.,

$$W_f = \frac{\beta_1}{\beta_2 + \phi_r} - K_f \quad \text{Eqn S3}$$

where

$$\beta_1 = \frac{Y \sigma_{fM} K_f}{(1/T_f) + r_m [N]_f n_r} \quad \text{Eqn S4}$$

$$\beta_2 = \frac{(1/T_f) + [N]_f (\alpha_w c_H / T_w) + Y r_m (1 + n_w \alpha_w c_H [N]_f)}{(1/T_f) + Y r_m [N]_f n_r} \quad \text{Eqn S5}$$

Similarly, since  $dW_N/dt = 0$  at steady state, the rate of N uptake is

$$U = [N]_f W_f \times \left( \frac{1 - f_f}{T_f} + \frac{(1 - f_r) n_r \phi_r}{T_r} + \frac{(1 - f_w) n_w \alpha_w c_H [N]_f}{T_w} \right) \quad \text{Eqn S6}$$

Substitution of (Eqn 9) yields steady state  $W_f$  from the nitrogen balance as a function  $\phi_r$  and  $[N]_f$ , i.e.,

$$W_f = \frac{\beta_3}{\beta_4 + \phi_r} - \frac{K_r}{\phi_r} \quad \text{Eqn S7}$$

where

$$\beta_3 = \frac{U_{\max}}{[N]_f (1 - f_r) n_r / T_r} \quad \text{Eqn S8}$$

$$\beta_4 = \frac{[(1 - f_f) / T_f] + [(1 - f_w) n_w \alpha_w c_H [N]_f / T_w]}{(1 - f_r) n_r / T_r} \quad \text{Eqn S9}$$

and  $U_{\max} \equiv \sigma_{fM} K_r$  is the maximum rate of N uptake, which must be specified.

Our objective is the determination of the masses of foliage and fine roots, and the foliar nitrogen concentration,  $[N]_f$ , that maximize the rate of production,  $G$ , subject to the equality of (Eqn S3) and (Eqn S7)—i.e., the foliage mass from the carbon balance must equal the foliage mass from the nitrogen balance.

Subtraction of (Eqn S7) from (Eqn S3) yields a cubic equation in  $\phi_r$  with either one or three real roots, i.e.,

$$\phi_r^3 + a_1 \phi_r^2 + a_2 \phi_r + a_3 = 0 \quad \text{Eqn S10}$$

where

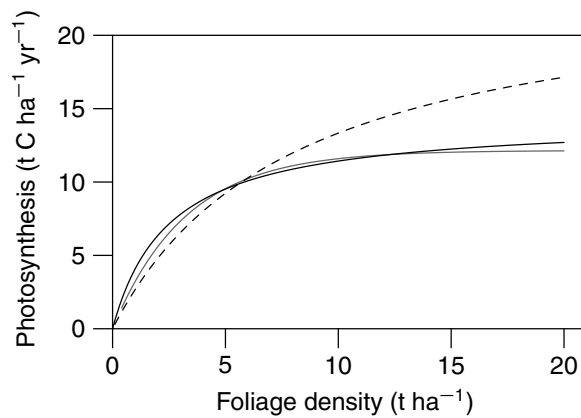
$$a_1 = \frac{\beta_1 - \beta_3 + K_r - K_f (\beta_2 + \beta_4)}{-K_f} \quad \text{Eqn S11}$$

$$a_2 = \frac{\beta_1 \beta_4 - \beta_2 \beta_3 + K_r (\beta_2 + \beta_4) - K_f \beta_2 \beta_4}{-K_f} \quad \text{Eqn S12}$$

$$a_3 = \frac{K_r \beta_2 \beta_4}{-K_f}. \quad \text{Eqn S13}$$

The root of interest is the value of  $\phi_r$  which maximizes  $G$ . Given  $[N]_f$ , the cubic equation provides  $\phi_r$  and, together,  $[N]_f$  and  $\phi_r$  provide  $W_f$  with either (Eqn S3) or (Eqn S7), and then  $[N]_f$ ,  $\phi_r$ , and  $W_f$  provide  $G$  with (Eqn S1). Thus, since  $[N]_f$  determines the values of  $\phi_r$  and  $W_f$ , the problem of maximizing  $G$  reduces to finding the value of  $[N]_f$  that maximizes  $G$ . This is accomplished by numerical search.

Nitrogen availability ( $\text{kg N (t fine root)}^{-1} \text{ yr}^{-1}$ ) is defined as the fine-root specific rate of N uptake,  $\sigma_{fM}$ . Thus, optimal model solutions over a gradient of N availability obtain from maximizing  $G$  over a range of specified values for  $U_{\max}$ .



**Fig. S1** Model solutions: Rate of photosynthesis versus foliage density: Scots pine (solid), Norway spruce (dash). Foliar N concentration is 1.4%. For comparison, a Lambert-Beer formulation is shown for pine (solid gray).

### Parameter values

The photosynthesis curve for pine comes from an analysis by Duursma & Mäkelä (2007), where a canopy photosynthesis model has been used to make a summary model of the Lambert-Beer type. The present model has been parameterised to be consistent with the Lambert-Beer model, assuming that the average specific leaf area is  $14 \text{ m}^2 \text{ kg}^{-1}$  (Juurola, 2003). The curve for Norway spruce has been parameterised to give a more steady increase in photosynthesis with increasing foliage mass, but with a lower initial capacity. This describes the more shade-tolerant character of Norway spruce compared with Scots pine (Figure S1).

Foliage retention in southern Finland is approximately 3.3 years in pine (Vanninen & Mäkelä, 1999) and 7–9 years in spruce (Kantola & Mäkelä, 2006). Sapwood longevity is about 40 years in spruce and 60 years in pine (Longetaud *et al.*, 2006). We use lower values here to account for branch turnover, which is faster (Lehtonen *et al.*, 2004), and because sapwood may become disused before converting to heartwood, due to branch death and shedding (see, e.g., Longetaud *et al.*, 2006).

The parameter  $\alpha_w = W_w/(W_f L)$  from (Eqn 12) can be expressed as  $\alpha_w = \rho/(W_f/A_w)$ , where  $\rho$  is the bulk density of live wood,  $A_w$  ( $\text{m}^2$ ) is the cross-sectional area of sapwood at the base of the canopy, and  $W_f/A_w$  is the ‘pipe ratio.’ The pipe ratio is approximately constant at  $500 \text{ kg}(\text{m}^2 \text{ sapwood})^{-1}$  for pine in southern Finland (Berninger *et al.*, 2005) and about  $900\text{--}1000 \text{ kg}(\text{m}^2 \text{ sapwood})^{-1}$  for spruce (Kantola & Mäkelä, 2006). The parameter  $c_H$  was assigned values for pine and spruce that give reasonable tree heights relative to typical empirical values of across different sites.

The maintenance respiration rates are consistent with Ryan (1991) and assume that tissue respiration depends on tissue N concentration. Parameters related to relative tissue N concentrations were determined from the findings of Helmisaari (1992), and are somewhat approximate. For ex-

ample, it is commonly observed that  $[\text{N}]_r$  is lower than  $[\text{N}]_f$  (e.g., Helmisaari *et al.*, 2007), but here we assume the same concentration for both.

### Biomass and [N] data

Data from eight Norway spruce (*Picea abies* L. Karst.) and eight Scots pine (*Pinus sylvestris* L.) dominated stands across a climatic gradient in Finland were used for model testing (Helmisaari *et al.*, 2007). The details of the data can be found in the original publication, but a brief summary is given here.

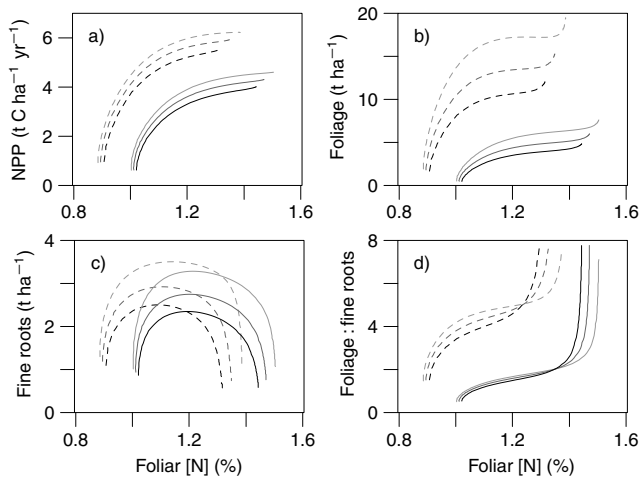
All the stands were situated in the boreal vegetation zone and represented relatively different site types and stages of stand development. The long-term (1961–1990) mean annual effective temperature sum (threshold  $+5^\circ \text{C}$ ) varied between 660 and 1351 degree days, and mean annual precipitation between 420 and 630 mm.

All stands had reached canopy closure. The age of the six relatively even-aged managed Norway spruce stands varied between 55 and 140 years, and the average age of the largest trees in two uneven-aged natural stands was 170 years. The age of the seven, relatively even-aged, managed Scots pine stands varied between 55 and 200 years, and the mean age of the one uneven-aged natural stand was 130 years. The site types (Cajander, 1949) varied from fertile herb-rich *Oxalis-Myrtillus* (OMT) types in southern Finland to nutrient-poor xeric *Calluna* (CT), and *Empetrum-Calluna* (ECT) types in the north. The soil types were mostly podzols.

Each stand contained three sub-plots,  $30 \times 30 \text{ m}$  in size. Stand measurements were made on all three sub-plots in each stand. Tree species, diameter (at 1.3 m above ground level), tree height and crown length were measured on all trees on the plot with a breast height diameter of at least 4.5 cm. This allowed accurate determination of individual tree volumes and basal areas, as well as respective stand level characteristics.

Fine root samples for biomass and nutrient determinations were taken in July–August 1998. From each stand, 12 root cores were taken from organic layer and 0–30 cm mineral soil layer. The roots were sorted into living and dead roots, and further into pine, spruce, birch and other broadleaved roots, and understorey based on microscopic morphology and colour. The roots smaller than 2 mm were regarded as fine roots (Persson, 1983; Vogt *et al.*, 1983), and they included mycorrhizal short root tips. The root samples were dried at  $70^\circ \text{C}$  for 48 h, then weighed and milled. Total nitrogen was determined on a CHN (Leco) analyser.

Needle biomass estimates for individual trees were calculated using the functions of Marklund (1987, 1988). These functions in most cases describe the biomass components as a function of tree species, diameter and tree height. However, the functions describing needle biomass for Norway spruce and Scots pine also include crown length as an additional explanatory variable. The needle mass function for Scots pine also includes the latitudinal coordinate.



**Fig. S2** Sensitivity of optimal model solutions to a 25% reduction in  $c_H$  (light gray), no change (medium gray), and a 25% increase (black): Scots pine (solid), Norway spruce (dash).

Needle nitrogen concentration of current-year needles was measured using composite samples from 10 sample trees per stand in October–November 1997. The samples were dried (60° C), weighed and milled and analysed for total nitrogen using the CHN (LECO CHN-600) analyser (Merilä *et al.*, 2007).

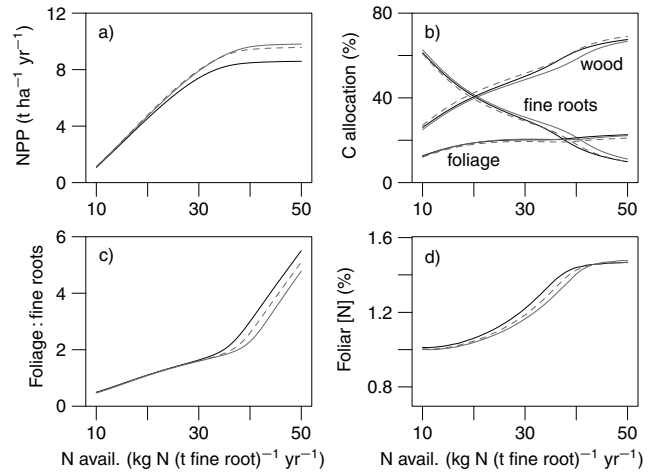
## Sensitivity of optimal solution to key parameters

### *Sensitivity to steady-state pipe length*

The realism of the model hinges upon the adequacy of our assumption of a steady-state pipe length and the parameter  $c_H$  that relates the steady-state pipe length to  $[N]_f$ . We therefore assessed the sensitivity of some model solutions to  $\pm 25\%$  changes in the standard value of  $c_H$  (Figure S2). The lower value of  $c_H$  causes an increase in the magnitude and range of the optimal steady-state values of NPP, foliage density, and fine root density versus  $[N]_f$ . Higher values have the opposite effects. However, the ratio of foliage to fine roots is little affected over the range of  $[N]_f$  values found in nature.

### *Sensitivity to maximum specific rate of photosynthesis*

Increasing  $CO_2$  availability in the atmosphere may increase the maximum specific rate of photosynthesis,  $\sigma_{FM0}$ , though the response in terms of GPP will depend upon how the steady-state pipe length responds to the increase in photosynthesis. We studied this by comparing two extreme responses in height growth: (1)  $L_{ss}$  remains dependent on  $[N]_f$  only, or (2)  $L_{ss}$  is increased through a proportional increase in  $c_H$ . The results for a 10% increase in  $\sigma_{FM0}$  are presented for pine only, but were essentially the same for spruce. In both cases, total production increases, the ratio of foliage to roots decreases at high N availability, and  $[N]_f$  decreases at moderate N availability, compared with the reference  $\sigma_{FM0}$  (Figure S3).



**Fig. S3** Optimal model solutions with the standard parameter set in Table 1 (black), a 10% increase in  $\sigma_{FM0}$ , the nitrogen-saturated specific rate of photosynthesis (gray), and a 10% increase in both  $\sigma_{FM0}$  and  $c_H$ , the ratio of average pipe length to foliar N concentration (gray dash).

There is a slight increase in allocation to fine roots for case (1) at moderate N availability. Responses are very small at low N availabilities and only become apparent when there is sufficient N to allow for the utilization of the increased availability of C. In both cases, NPP increases noticeably only where N availability is moderate to high. In case (1), increased root allocation occurs at the cost of woody growth, but allocation to wood is increased slightly in case (2). The implications of increasing the photosynthetic capacity were in line with previous studies (Hyvönen *et al.*, 2007; Mag-nani *et al.*, 2007), showing little impact on production at low N availability (Figure S3a). Moreover, the uncertainty about the response of height growth to increased photosynthetic capacity did not seem to influence the overall growth response to increasing photosynthesis. For forestry predictions, however, it would be crucial to know how height growth responds to environmental changes.

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