



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

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Summary

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• Nitrogen (N) is essential for plant production, but N uptake imposes carbon (C) costs through maintenance respiration and fine-root construction, suggesting that an optimal C:N balance can be found. Previous studies have elaborated this optimum under exponential growth; work on closed canopies has focused on foliage only. Here, the optimal co-allocation of C and N to foliage, fine roots and live wood is examined in a closed forest stand.

• Optimal co-allocation maximizes net primary productivity (NPP) as constrained by stand-level C and N balances and the pipe model. Photosynthesis and maintenance respiration increase with foliar nitrogen concentration ([N]), and stand-level photosynthesis and N uptake saturate at high foliage and fine-root density.

• Optimal NPP increases almost linearly from low to moderate N availability, saturating at high N. Where N availability is very low or very high, the system resembles a functional balance with a steady foliage [N]; in between, [N] increases with N availability. Carbon allocation to fine roots decreases, allocation to wood increases, and allocation to foliage remains stable with increasing N availability.

• The predicted relationships between biomass density and foliage [N] are in reasonable agreement with data from coniferous stands across Finland. All predictions agree with our qualitative understanding of N effects on growth.

Key words: allocation, carbon and nitrogen, forest, functional balance, growth model, optimization, productivity and biomass, steady state.

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Introduction

Nitrogen (N) availability is crucial for forest production, but N uptake imposes carbon (C) costs for fine-root construction (Davidson, 1969) and maintenance respiration (Ryan, 1991). This suggests that an optimal pattern of C and N co-allocation exists. In an evolutionary sense, nature may select for plants that optimize their use of available resources and achieve high productivity. In this regard, it has been suggested that a model of optimal co-allocation of N and C production could advance our understanding of plant responses to variable N and C supplies (Johnson & Thornley, 1987; Mäkelä & Sievänen, 1987; Hilbert, 1990; McMurtrie, 1991; Dewar, 1996; Ågren & Franklin, 2003; Franklin, 2007).

The results of optimization studies largely depend on the assumptions used to constrain the problem. A balanced-growth approach is based on the assumption that the tissue N concentration is maintained at a 'balanced level' by optimal allocation of substrate to shoots and roots. The assumption that allocation controls the balance essentially relies, in turn, on the assumption that shoot and root activities in C and N acquisition depend on organ size. The balanced level may be either an *a priori* assumption reflecting a demand for N defined by the stoichiometries of the shoot and root tissues (Mäkelä & Sievänen, 1987), or an additional result of the optimization problem, based on additional assumptions concerning the impacts of N on growth and production (Johnson & Thornley, 1987; Hilbert, 1990; Ågren & Franklin, 2003).

Hilbert (1990) showed that, if the rate of photosynthesis was a saturating function of the N concentration in leaves, then the optimal concentration varied smoothly with N availability. Optimal allocation was a compromise between N costs incurred by C allocation to roots, and N gain from an increase in photosynthesis due to increased N concentration in leaves.

The above studies were confined to analysing unconstrained, exponential growth, defining relative growth rate as the objective function to be maximized. Other investigators have analysed optimal steady-state canopies, where leaf N concentration impacts physiological processes (McMurtrie, 1991; Dewar, 1996; Franklin & Ågren, 2002; Franklin, 2007). However, the cost of N acquisition is absent from these models. McMurtrie (1991) assumed a canopy connected to a root system sufficient for the uptake of all available N. Dewar (1996) derived an optimal canopy N content for a given leaf area index (LAI), and Franklin (2007) derived an optimal leaf area index for a given N content, but no explicit cost was attached to the construction or maintenance of the root system that would be required to acquire the assumed N content.

The cost of constructing a root system is explicit in the balanced-growth models, but the exponential-growth studies have implicitly assumed that the requirement for N can always be satisfied by suitable growth allocation to roots, regardless of the size of the plant. At the stand level, this assumption must be tempered by the reality of limited N availability.

In forest stands, the limitation of resources leads to closed, or nonexpanding, canopies. These situations can be analysed effectively by considering the C and N balances of the stand at steady state (Dewar, 1996; Franklin, 2007). Strictly speaking, the steady-state assumption does not apply to woody biomass, as stem elongation continues until stand senescence (Mäkelä & Valentine, 2001). However, the elongation growth utilizes a small fraction of net primary productivity (NPP) (Mäkelä, 1986), so, at appropriate timescales, the steady-state assumption can nevertheless serve as a realistic approximation for resource-limited stands.

The objective of this study was to explore the extent to which optimal co-allocation of C and N at steady state explains observed responses of forest traits to variable N and C supply and climate. Do optimal closed-canopy foliage density and above-ground allocation increase with N availability? How do these patterns interact with leaf N concentration and canopy height? Is light use efficiency (LUE) independent of N availability? How do optimized stands respond to increasing atmospheric CO₂? Is there a climate-independent relation among foliage density, fine-root density and leaf N concentration?

We consider these questions by means of a model that maximizes net production at steady state by optimizing the co-allocation of C and N to leaves, fine roots, and live wood, given the maximum uptake rate of N, and accounting for the costs of production and maintenance respiration.

Description

C and N balances

Consider the aggregate biomasses of foliage, fine roots, and live wood in a stand of trees. Denote the respective dry matter densities (kg ha⁻¹) by W_f , W_r , and W_w , and their tissue N concentrations (kg N (kg component)⁻¹) by $[N]_f$, $[N]_r$, and $[N]_w$.

Let G be the rate of production of new dry matter (kg ha⁻¹ yr⁻¹), and let λ_f , λ_r , and λ_w , respectively, be the proportional allocation of production to foliage, fine roots, and live wood, where $\lambda_f + \lambda_r + \lambda_w = 1$. The growth rates (kg ha⁻¹ yr⁻¹) of the dry matter components are

$$\frac{dW_f}{dt} = \lambda_f G - \frac{W_f}{T_f} \quad \text{Eqn 1}$$

$$\frac{dW_r}{dt} = \lambda_r G - \frac{W_r}{T_r} \quad \text{Eqn 2}$$

$$\frac{dW_w}{dt} = \lambda_w G - \frac{W_w}{T_w} \quad \text{Eqn 3}$$

where T_f , T_r , and T_w are the respective average longevity (yr) of tissue.

From a C balance perspective, the rate of dry matter production is

$$G = Y(P - R_m) \quad \text{Eqn 4}$$

where P (kg C ha⁻¹ yr⁻¹) is the rate of photosynthetic production, R_m (kg C ha⁻¹ yr⁻¹) is the rate of maintenance respiration, and Y (kg component (kg C)⁻¹) is the conversion efficiency of C to dry matter in growth, including growth respiration. Maintenance respiration by component is proportional to the tissue N concentration, and therefore

$$R_m = r_m [N]_f W_f + r_m [N]_r W_r + r_m [N]_w W_w \quad \text{Eqn 5}$$

where r_m (kg C (kg N)⁻¹ yr⁻¹) is the N-specific respiration rate (Ryan, 1991).

Stand photosynthesis is usually described by an exponential function that follows from the Lambert–Beer law (McMurtrie, 1991). This function is accurately approximated with a rectangular hyperbola which is mathematically more simple, promoting wider understanding of the model and allowing for straightforward calculations. We therefore model the rate of photosynthesis of the stand, P , as

$$P = \frac{\sigma_{fM} W_f K_f}{W_f + K_f} \quad \text{Eqn 6}$$

where σ_{fM} (kg C (kg foliage)⁻¹ yr⁻¹) is the light-saturated foliage-specific rate of photosynthesis, and K_f (kg ha⁻¹) is the density of foliage dry matter that reduces the rate to 50% of

the light-saturated rate. This also provides a saturating dependence of the rate of photosynthesis on LAI, because $LAI = W_f \times SLA$, where SLA is the specific leaf area. The light-saturated specific rate of photosynthesis is a function of foliar N concentration (Field & Mooney, 1986):

$$\sigma_{fM} = f([N]_f) \quad \text{Eqn 7}$$

Denote by W_N the areal density of N in the stand (kg N ha^{-1}). The N balance of the stand is

$$\frac{dW_N}{dt} = U - \frac{(1-f_f)[N]_f W_f}{T_f} - \frac{(1-f_r)[N]_r W_r}{T_r} - \frac{(1-f_w)[N]_w W_w}{T_w} \quad \text{Eqn 8}$$

where U ($\text{kg N ha}^{-1} \text{ yr}^{-1}$) is the N uptake rate, and f_p, f_r and f_w are the fractions of tissue N resorbed from senescent tissues. We assume that the N concentrations of fine roots and live wood are proportional to that of foliage, that is, $[N]_r = n_r [N]_f$ and $[N]_w = n_w [N]_f$ where n_r and n_w are constant.

The N uptake rate, U , is also modelled using the rectangular hyperbola:

$$U = \frac{\sigma_{rM} W_r K_r}{W_r + K_r} \quad \text{Eqn 9}$$

where σ_{rM} ($\text{kg N (kg fine root)}^{-1} \text{ yr}^{-1}$) is the maximum fine-root-specific N uptake rate which depends on the availability of N in the soil. K_r is analogous to K_f of Eqn 6.

Dependence of photosynthesis on N concentration

We assume that the light-saturated specific rate of photosynthesis, σ_{fM} , is a saturating function of the photosynthetic N in leaf tissue (Field & Mooney, 1986; Hilbert, 1990; Ågren & Franklin, 2003; Ellsworth *et al.*, 2004), that is,

$$\sigma_{fM} = \frac{\sigma_{fM0} [N]_p}{[N]_p + [N]_{ref}} \quad \text{Eqn 10}$$

where σ_{fM0} ($\text{kg C (kg foliage)}^{-1} \text{ yr}^{-1}$) is the N-saturated specific rate of photosynthesis, $[N]_{ref}$ is the concentration of photosynthetic N for which $\sigma_{fM} = \sigma_{fM0}/2$, and $[N]_p$ is the actual photosynthetic N concentration in foliage, defined as

$$[N]_p = \max\{[N]_f - [N]_0, 0\} \quad \text{Eqn 11}$$

where $[N]_0$ is the concentration of nonphotosynthetic, or structural, N in the foliage.

Woody mass: pipe model

We assume that trees follow the pipe model, so the mass of live wood is related to foliar mass and mean pipe length, $L(m)$, by

$$W_w = \alpha_w W_f L \quad \text{Eqn 12}$$

where α_w (m^{-1}) is constant (Valentine, 1985). It follows from this assumption that otherwise similar stands with tall trees have a lower ratio of foliage to total respiring biomass than stands with shorter trees (Mäkelä & Valentine, 2001). The rate of production of live wood dry matter is $G_w = \lambda_w G$, a fraction of which is attributable to elongation of shoots and roots, and the remaining fraction to the expansion or thickening of stems. Let η ($0 < \eta \leq 1$) and $1 - \eta$, respectively, be the fractions of wood production from expansion (G_{wd}) and elongation (G_{ws}).

Steady state and pipe model

Foliar and fine-root biomass and the aggregate cross-sectional area of live wood ordinarily achieve an approximate steady state after a stand closes, but stem elongation continues until stand senescence (Mäkelä & Valentine, 2001). However, on an appropriate timescale (say, 5–10 yr for boreal conifers near canopy closure) the height growth term is very small relative to the other terms. We therefore consider a quasi-steady state where $G_w \approx W_w / T_w$, which means that the height growth term is neglected ($\eta = 1$), and new wood is produced at approximately the same rate at which old live wood deactivates.

The elimination of all elongation has no effect on the C balance at quasi-steady state, because the missing elongation fraction of the wood production is accounted for by a commensurate increase in the expansion fraction. The resultant constant mean pipe length is denoted by L_{ss} .

At quasi-steady state, we require that growth equals litter production for all biomass components:

$$\lambda_i G = \frac{W_i}{T_i}, \quad i = f, r, w \quad \text{Eqn 13}$$

and, secondly, that N uptake equals N loss:

$$U = \frac{(1-f_f)[N]_f W_f}{T_f} + \frac{(1-f_r)[N]_r W_r}{T_r} + \frac{(1-f_w)[N]_w W_w}{T_w} \quad \text{Eqn 14}$$

Finally, we need to express mean pipe length at quasi-steady state as a function of site quality, as described by the metabolic parameters and/or state variables in a stand. Tree height growth is known to respond strongly to N availability. Following Thornley (1991), we assume that height growth and, therefore, mean pipe length at quasi-steady state are proportional to $[N]_f$:

$$L_{ss} = c_H [N]_f \quad \text{Eqn 15}$$

where c_H is a parameter. Previous derivations from the pipe model have shown that the maximum achievable height (asymptotic steady state) depends on the availabilities of both

Table 1 Values for parameters used in the simulations

Parameter	Definition	Pine (<i>Pinus sylvestris</i>)	Spruce (<i>Picea abies</i>)	Units
K_r	Amount of roots capturing 50% of available N	2000	2000	kg ha ⁻¹
K_f	Amount of foliage capturing 50% of maximum C gain	2500	8000	kg ha ⁻¹
T_f	Mean lifetime of foliage	3.3	8	yr
T_r	Mean lifetime of fine roots	1.25	1.25	yr
T_s	Mean lifetime of sapwood	40	33.3	yr
Y_g	Growth efficiency	1.54	1.54	kg DW kg ⁻¹ C
r_m	Specific rate of maintenance respiration	16	16	kg ⁻¹ N yr ⁻¹
σ_{fMO}	N-saturated specific rate of photosynthesis	8.0	4.0	kg C kg ⁻¹ DW yr ⁻¹
n_r	Ratio of fine-root [N] to foliage [N]	1	1	–
n_w	Ratio of sapwood [N] to foliage [N]	0.07	0.07	–
$f_i, i = f, r, w$	Proportion [N] recycled	0.3	0.3	–
α_w	Sapwood weight per unit foliage and pipe length	0.8	0.4	m ⁻¹
c_H	'Steady-state' pipe length coefficient	2800	3400	m kg ⁻¹ N kg DW
$[N]_0$	Structural [N]	0.009	0.008	kg N kg ⁻¹ DW
$[N]_{ref}$	Reference photosynthetic [N]	0.002	0.002	kg N kg ⁻¹ DW

DW, dry weight.

C and N symmetrically (Mäkelä, 1986; Valentine, 1997). Here we have ignored the dependence of L_{ss} on the availability of C, focusing on the effect of site quality on steady-state height within one climatic region. The effect of C availability at a particular site is therefore embedded in the parameter c_H . The choice of c_H also reflects the stand age at which the quasi-steady state is considered. Under pipe model assumptions, otherwise similar stands with tall trees have a lower ratio of foliage to total respiring biomass than stands with shorter trees.

Optimal N concentration and allocation at steady state

Optimization problem Using the above assumptions, our objective is to determine the masses of foliage and fine roots and the foliar N concentration, $[N]_f$, under the steady-state conditions of the model. The steady-state assumptions follow from the C and N balance (Eqns 13–14). However, solving these equations will only yield two of the three unknowns. An additional constraint is obtained by maximizing the rate of production, G . Formally, we solve the following optimization problem:

$$\text{Max}\{G([N]_f, W_f, W_r)\} \quad \text{Eqn 16}$$

$$\text{Subject to } \frac{dW_N}{dt} = 0, \frac{dW_i}{dt} = 0, i = f, r, w.$$

The solution of the problem in Eqn 16 is an optimal compromise between the C gain of increasing $[N]_f$ through increased photosynthesis and the C costs of high $[N]_f$ produced by maintenance respiration and fine-root construction, in a situation where the availability of either C or N or both may become limiting. Details of the solution are provided in the [Supporting Information](#).

Parameter values

We assigned plausible values to the parameters of the model for Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L.), although no statistical fitting of the model was attempted for either species (Table 1). There were differences between pine and spruce in the $P(W_f)$ curve, foliage, fine-root and live wood longevities, the wood growth parameters α_w and c_H , and the assumed concentration of structural N in foliage. See [Supporting Information](#) for details of the parameter values.

Under boreal conditions, differences in growth between sites of different geographical location but similar site type are mainly attributable to differences in growing season length and temperature. The effective temperature sum (ETS) with threshold 5°C is customarily used to quantify this. We assume that all metabolic parameters, c_i , scale linearly with ETS, that is:

$$c_i = c_{i0} \left(\frac{\text{ETS}}{\text{ETS}_{ref}} \right) \quad \text{Eqn 17}$$

where c_{i0} is the value of c_i at ETS_{ref} . The parameters scaled in this way are the specific rates σ_{fMO} , σ_{rMP} , and r_m , the reciprocal tissue longevities T_f^{-1} , T_r^{-1} , and T_w^{-1} , and the steady-state height parameter c_H . Measurements of Scots pine across a climate gradient from southern Europe to Lapland also indicate that the inverse of the pipe model parameter α_w scales approximately in proportion to ETS from south to north (Palmroth *et al.*, 1999).

Results

In this section, we explore the implications of the model concerning responses of forest traits to variable N supply and climate, focusing on the questions presented in the Introduction.

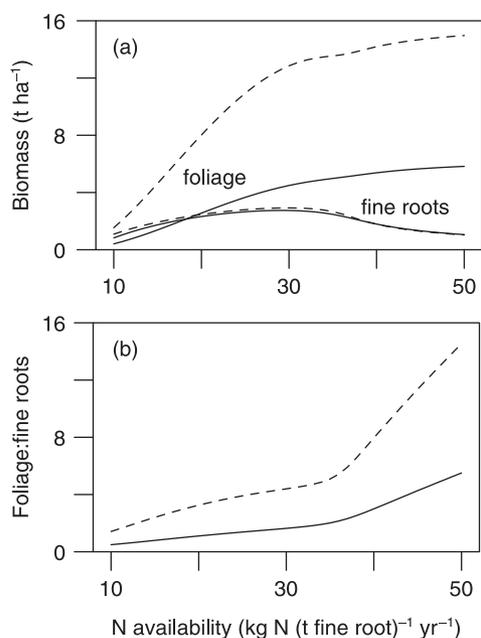


Fig. 1 Model solutions. (a) Foliage and fine-root densities that maximize productivity given the nitrogen (N) availability: Scots pine (*Pinus sylvestris*), solid line; Norway spruce (*Picea abies*), dashed line. (b) The corresponding ratios of foliage to fine roots.

Firstly, we analyse how variable N supply affects optimal foliage and fine-root densities, leaf [N], plant production and C allocation at steady-state. N availability is quantified as the maximum fine-root-specific rate of N uptake, σ_{rM} . Secondly, we explore the impacts of climate, measured as variable ETS, on the relationship between foliage and fine-root density and leaf [N]. A comparison with measurements (see [Supporting Information](#) for details) is provided in the latter case. How the assumed steady-state height affects the results, and what happens when the maximum photosynthetic rate increases, for example as a result of increased atmospheric CO₂ concentration, are analysed in the [Supporting Information](#).

The effect of N availability on optimal steady state

Foliage and fine-root mass The model indicates that optimal steady-state foliage density increases in a saturating manner from low to high N availability. Optimal steady-state fine-root density increases to a maximum from low to moderate N availability, and then decreases as N availability increases further (Fig. 1a). The foliage to fine-root ratio first increases moderately with increasing N to the point at which fine-root density starts to decrease with increasing N availability. From this point, the ratio increases more rapidly per unit increase in σ_{rM} (Fig. 1b).

The foliage density is much greater in spruce than in pine, as a result of greater shade tolerance, as quantified by the parameter K_p and greater foliage longevity, T_f . The parameter

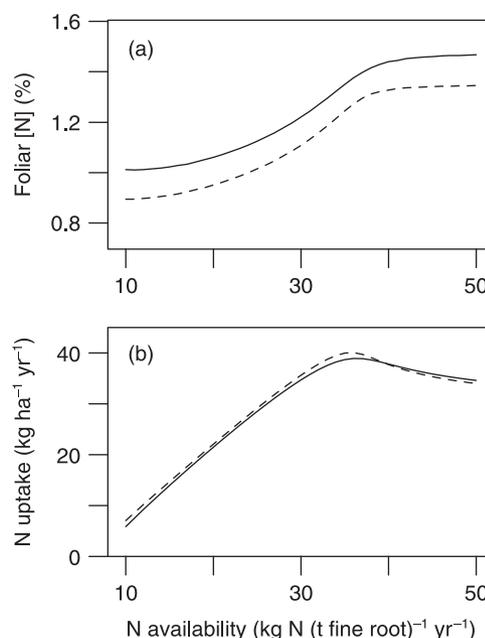


Fig. 2 Model solutions. (a) Nitrogen (N) concentration in foliage that maximizes productivity given the foliage density in Fig. 1(a) and the N availability: Scots pine (*Pinus sylvestris*), solid line; Norway spruce (*Picea abies*), dashed line. (b) The corresponding rate of N uptake by a stand with the foliage and fine-root densities in Fig. 1(a).

values for fine-root longevity and nutrient uptake are similar in spruce and pine, so the predicted fine-root densities are also similar in the two species.

Tissue [N] and N uptake The optimal steady-state N concentration in the foliage, $[N]_f$ is an S-shaped function which starts to plateau at the level of N availability that corresponds to the turning point in the foliage to fine-root ratio (Fig. 2a). At very low N availability, any gain in N uptake achieved through an investment in fine-root production is quickly utilized in further foliage production, affording only a small increase in $[N]_f$ with increasing N availability. Where rapid N uptake is possible, an increase in $[N]_f$ has little effect on production because of increased respiration, and because any tendency toward an increase in $[N]_f$ is checked by less investment to fine roots.

The model indicates that pine maintains a higher tissue [N] than spruce at any given level of N availability. The difference relates to the different parameter values for the nonphotosynthetic [N] in spruce and pine. Note that, in the optimal solution, total N uptake peaks at a moderate level of N availability, and is lower where N is readily available (Fig. 2b), primarily because gross production is limited by light where N availability is high (Fig. 3a). It is therefore optimal to maintain the canopy N concentration, $[N]_f$ at a level independent of any further increase in N availability: the greater the availability of N, the smaller the fine-root density required to supply the required

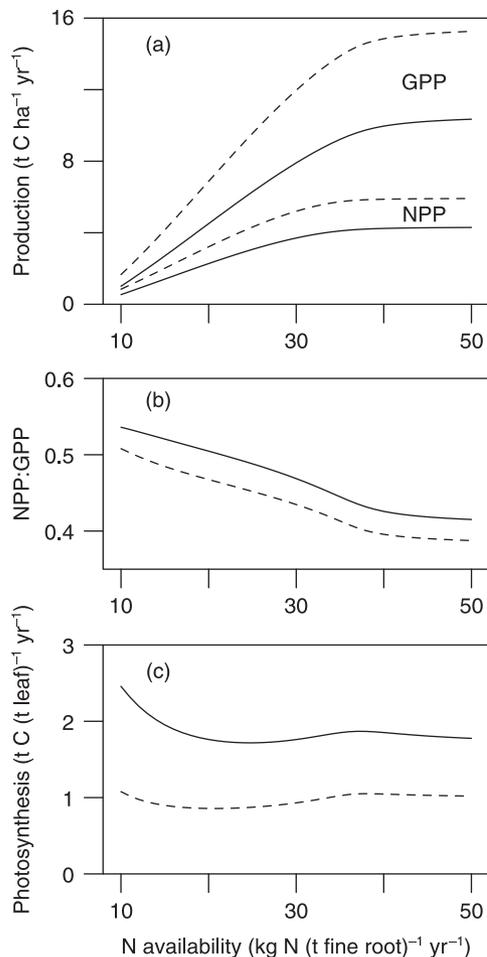


Fig. 3 Model solutions. (a) The maximum rates of gross and net primary production (GPP and NPP): Scots pine (*Pinus sylvestris*), solid line; Norway spruce (*Picea abies*), dashed line. (b) The corresponding ratios of NPP to GPP, and (c) the corresponding leaf specific rates of photosynthesis.

canopy N. Because the density of fine-roots is diminished, the consumption of N by fine roots also is diminished, reducing the optimum uptake of N with increasing N availability.

Carbon assimilation and NPP Both gross primary production (GPP) and NPP first increase with increasing N availability, and then saturate when light becomes limiting (Fig. 3a). The ratio of NPP to GPP decreases as a function of increasing N availability, because production is not increased as much as respiration (Fig. 3b). The increase in respiration relative to production is a result of increased $[N]_p$ and increased tree height relative to foliage, according to the assumption of Eqn 15 in combination with the pipe model (Eqn 12).

The model indicates that the foliage-specific photosynthetic rate is fairly constant across sites, although both foliage density and $[N]_f$ increase with increasing N availability (Fig. 3c). Apart from sites with really low N availability, the shading effect is

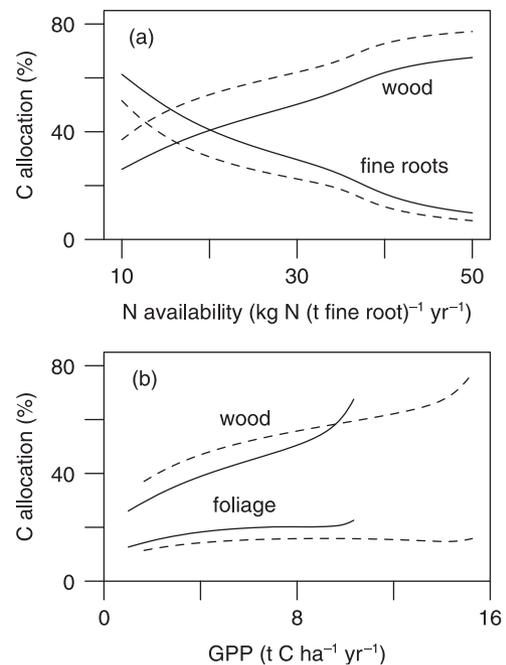


Fig. 4 Model solutions. (a) Fractions of the net production allocated to wood and fine roots given the nitrogen (N) availability: Scots pine (*Pinus sylvestris*), solid line; Norway spruce (*Picea abies*), dashed line. (b) The fractions of net production allocated to foliage and wood, given the corresponding gross primary productivity (GPP).

largely compensated by an increase in $[N]_p$ which increases the photosynthetic capacity.

Allocation of production In both species, the model indicates that allocation of production to wood increases with increasing N availability (Fig. 4a). At the same time, allocation to foliage remains relatively constant. In other words, the decrease in allocation to fine roots with increasing N availability is not compensated by allocation to foliage but rather by increased allocation to wood (Fig. 4a). This implies that allocation to wood increases and allocation to fine roots decreases with increasing productivity (Fig. 4b). Higher productivity leads to taller trees that require more allocation to wood than do shorter trees.

Effect of climate: comparison of model and data

The model indicates that decreasing ETS reduces NPP and GPP at moderate to high levels of N availability (Fig. 5a). Because N is less available at lower ETS (Eqn 17), a reduction in ETS causes the curves of biomass density against N availability to shift towards lower N availabilities (Fig. 5b). A similar shift occurs in the ratio of foliage to fine roots (Fig. 5c) and $[N]_f$ (Fig. 5d). These results imply that, while net production increases with ETS for fixed $[N]_f$ (Fig. 5e), the dependence of foliage and fine-root density on $[N]_f$ is insensitive to ETS (Fig. 5f). This allows us to compare predicted foliage and fine-root densities with field estimates across different climatic regions.

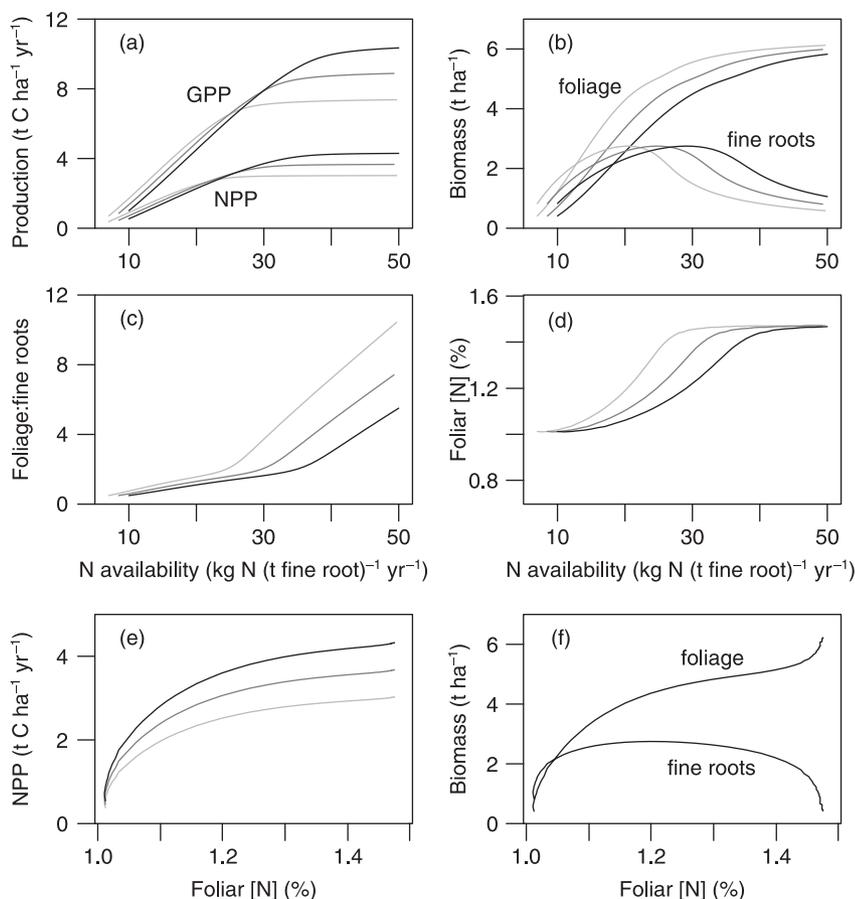


Fig. 5 Optimal model solutions with the standard parameter set in Table 1 (black), a 15% reduction in the effective temperature sum (ETS) (medium grey), and a 30% reduction in ETS (light grey). ETS affects both productivity (a, e) and allocation (c). Note, however, that optimal foliage and fine-root densities (b) and the optimal nitrogen (N) concentration (d) are shifted proportionally with respect to N availability by a change in ETS. Consequently, optimal foliage and fine-root density versus optimal N concentration is unaffected by a change in ETS (f).

Field estimates for comparisons were obtained for eight stands dominated by Norway spruce and another eight stands dominated by Scots pine across a climatic gradient in Finland (Helmisaari *et al.*, 2007). The stands represented different site types and stages of stand development, and they were all situated in the boreal zone, with ETS varying between 660 and 1290 degree-days. A summary of the data can be found in the [Supporting Information](#).

In both species, $[N]_f$ was a good indicator of the ratio of foliage to fine roots (Fig. 6a), although there was considerable scatter in the data for both foliage (Fig. 6b) and fine-root (Fig. 6c) densities. Nevertheless, the predicted order of magnitude and general patterns were consistent with the data.

Discussion

We have formulated an optimization model of the co-allocation of C and N in stands of trees with steady-state canopies. The model assumes an N dependence of photosynthesis and maintenance respiration, and accounts for the C cost of fine-root construction. The effect of crowding on both photosynthesis and N uptake is incorporated through the saturation of metabolic rates with biomass density. The model

also accounts for the C demand of wood production, which accords with the pipe model.

Previous models have employed different subsets of these assumptions. The present results are consistent with those from previous studies, where assumptions overlap. For example, the optimal steady-state foliage density and the related $[N]_f$ increase with increasing N availability (McMurtrie, 1991; Dewar, 1996; Franklin & Ågren, 2002; Franklin, 2007), the ratio of foliage to fine roots and above-ground allocation increase with increasing N supply (Mäkelä & Sievänen, 1987; Hilbert, 1990; Ågren & Franklin, 2003), and the impact of increased CO₂ supply depends on the simultaneous N availability ([Supporting Information](#); McMurtrie, 1991; Franklin, 2007). In addition, however, this study has provided more quantitative detail than previous studies about forest traits at steady state, as well as some predictions that are qualitatively new and in part surprising.

By combining the steady-state assumptions with the cost of fine-root construction, we were able to derive, from the structural and physiological characteristics of the species, a quantitative relationship between the maximum foliage and fine-root densities and N availability. These predictions are of the same order of magnitude as data-based densities from stands across

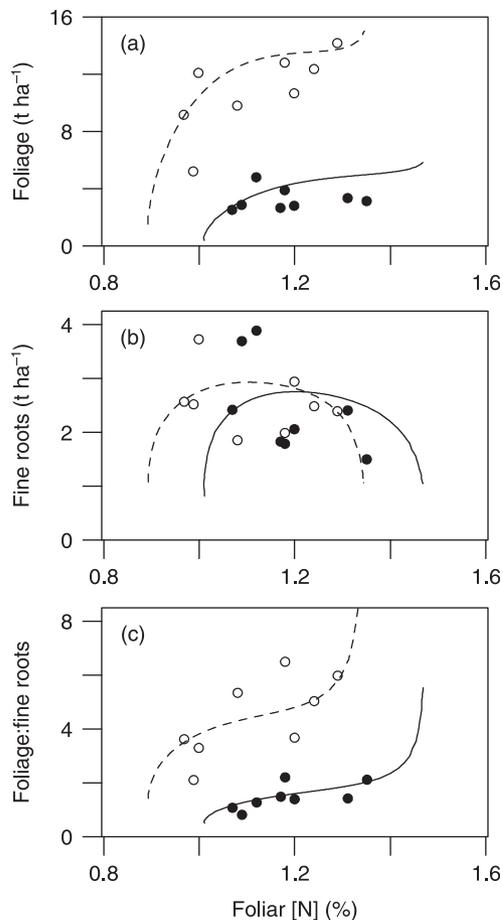


Fig. 6 Optimal model solutions and sample-based estimates from real stands for (a) foliage density, (b) fine-root density, and (c) the ratio of foliage to fine-root density versus N concentration in foliage: Scots pine (*Pinus sylvestris*), solid line, closed circles; Norway spruce (*Picea abies*), dashed line, open circles.

Finland. They also show a consistent pattern versus $[N]_f$, except at sites with the lowest $[N]_f$ where the estimates of fine-root density appear larger than predicted. This may be because the fine-root $[N]$ is assumed to be proportional to $[N]_p$ but observations indicate that the ratio of $[N]_r$ to $[N]_f$ is smaller at the poorest sites (Helmisaari *et al.*, 2007). This affords a greater fine-root density per unit available N.

As expected, the predicted foliage to fine-root ratio increases across sites as a function of N availability, but the slope of this relationship is steepest where N is so readily available that light becomes limiting (Fig. 2). Consistent with the presumption that boreal coniferous stands are generally N limited (Tamm, 1991), none of the observed stands fell within this range. However, such stands are needed to test the model, as factors other than N may require the maintenance of a root system larger than predicted in very fertile sites (Litton *et al.*, 2007).

Most previous studies on functional balance do not distinguish between total above-ground biomass and foliage biomass,

with the general conclusion that increasing allocation to fine roots should imply decreasing allocation to foliage (Mäkelä & Sievänen, 1987; Hilbert, 1990). Failure to observe this predicted behaviour in nature has led to hybridization of functional balance and allometric partitioning theories (McCarthy & Enquist, 2007). However, by splitting the above-ground biomass between foliage and wood in the present model, we found that N availability has little effect on the fraction of assimilate allocated to the production of foliage, although the fraction allocated to fine roots is greatest, and that to wood is least, at low levels of N availability. This seemingly surprising conclusion is supported by a recent empirical study which found that allocation to wood increases while the allocation to foliage remains fairly constant across increasing productivity classes (Litton *et al.*, 2007). The model provides these results as a consequence of the use of the pipe model and the assumption that the 'quasi-steady-state' height increases with increasing $[N]_p$ requiring more allocation to wood relative to foliage. At the same time, however, the productivity of the foliage is enhanced through increasing $[N]_p$ allowing the stand to support more foliage per unit area.

Regarding the effect of $[N]_f$ on net production in a stand, the model implies two limiting phases of behaviour. Where the level of N availability is low, the N uptake rate largely determines the production rate, and the allocation of C and N for the production of foliage and fine roots is finely tuned to maximize photosynthesis. Conversely, where N availability is high, the marginal benefit of increased $[N]_f$ is very small so $[N]_f$ approaches an upper limit, and production saturates with foliage density, which is indicative of light limitation. This leads to a pattern with two different steady $[N]_f$ concentrations, one at each end of the range of N availability, while in between, $[N]_f$ increases with N availability (Fig. 2). This kind of a pattern has not been predicted by previous optimization models, but it is in agreement with recent empirical findings (Le Maire *et al.*, 2005), and similar assumptions have been applied in phenomenological models (Running & Gower, 1991). The result largely follows from the assumptions that some of the N content is structural, and that the photosynthetic rate saturates over a fairly narrow range of the free N content. Although supported by empirical evidence qualitatively (Field & Mooney, 1986; Ellsworth *et al.*, 2004), the parameter values of this relationship remain uncertain.

The result that productivity per unit foliage mass depends on $[N]_f$ and foliage density implies that optimum steady-state canopies have very similar foliage-specific production rates regardless of N availability. At fertile sites, increased $[N]_f$ compensates for the loss of productivity caused by increased shading (Fig. 3c), which means that light use efficiency is predicted to increase. This result is consistent with observations from pine sites with variable fertility (Helmisaari *et al.*, 2002; Ladanaï & Ågren, 2004; Vanninen & Mäkelä, 2005), and sites across geographical gradients (Ollinger & Smith, 2005; Mäkelä *et al.*, 2008) and fertilization treatments (Gower *et al.*, 1992). By

contrast, Dewar (1996) found that the optimum N content (g N m^{-2} ground) of a stand should be proportional to absorbed photosynthetically active radiation, leading to decreasing $[\text{N}]_f$ with increasing leaf area index. However, Dewar (1996) did not consider the dependence of N uptake on soil N supply or root allocation.

Our simulations suggest that the relationship between $[\text{N}]_f$ and optimal steady-state biomass densities may be independent of climate, although the actual growth and production rates vary widely (Fig. 6). This result is consistent with empirical estimates of biomass density and $[\text{N}]_f$ across Finland, but relies upon the assumption that the key structural and metabolic parameters are controlled by ETS. Any increase in temperature is likely to have impacts similar to the geographical variation and its dependence on ETS. However, the tendency of the pipe model ratio to decrease with increasing ETS (Palmroth *et al.*, 1999) may be a genetic rather than phenotypic trait. This also means that the productivity response to changing ETS from climatic warming at a location may not be as pronounced as the differences in productivity attributable to geographic variation in ETS at any given time.

We adopted saturating rectangular hyperbolas to describe N uptake and photosynthetic production. The rectangular hyperbola is almost identical to the Lambert–Beer model of photosynthesis. N uptake has often been assumed to be efficient enough for the trees to utilize virtually all available N (Ågren, 1985; McMurtrie, 1991). This pattern might be described more accurately by a nonrectangular hyperbola providing abrupt saturation at a particular fine-root density.

In summary, the results seem consistent with several observed traits related to the C and N balance of trees, and explain different modes of behaviour in a range of environments. This suggests that optimization can be a powerful tool for analysing balancing interactions in plants (Mäkelä *et al.*, 2002). However, as we have pointed out, uncertainties remain regarding the constraints of the problem. In addition, what to maximize is not self-evident. Previous studies have applied a range of objective functions as surrogates for individual fitness or survival, including relative growth rate (Hilbert, 1990), photosynthetic production (Dewar, 1996), seed production (Iwasa *et al.*, 1985), expected net production over lifetime (Mäkelä & Sievänen, 1992), and growth (Franklin, 2007).

In this study, we chose to maximize stand-level net production at steady state. In closed stands, the productivity of the larger trees drives self-thinning: the greater the productivity, the faster the self-thinning of the shorter, least productive trees. These well-known stand dynamics provide some justification for our choice of the objective function. However, these same dynamics might seem to be at odds with our formulation of a steady-state, rather than a dynamic, model. However, a steady-state model provides relatively straightforward theory with which to interpret results from experiments and inventory efforts, although the theory may not apply to transient effects of experimental treatments.

Although the quasi-steady state for live woody biomass can only be assumed to hold for short periods at a time, the qualitative behaviour of the model is not sensitive to the choice of L_{ss} (Supporting Information). Our analysis indicated that the optimal steady-state NPP was largely insensitive to height, the variation in L_{ss} mainly affecting the allocation of production between foliage and wood. This suggests that height growth may not be solvable from the N optimization problem as such, justifying the quasi-steady-state assumption. Previous studies have considered height growth patterns as adaptive responses to competition between trees (Iwasa *et al.*, 1985; Mäkelä, 1985; King, 1986), and to self-shading within crowns (Mäkelä & Sievänen, 1992). Combining optimal N allocation and height growth in one model remains a challenge for future research.

To whatever use this model is put, its predictions should be viewed with a degree of scepticism. The success of the model will hinge upon whether natural selection yields aggregations of trees that optimize their co-allocation of C and N to maximize productivity. At this stage of research, we can state that the maximization hypothesis seems very plausible, where production is limited by N or light.

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Supporting Information

Additional supporting information may be found in the online version of this article.

The supporting information consists of more detailed descriptions of (1) the optimization method, (2) parameter values, (3) the stand foliage and fine-root data, and (4) the sensitivity of the model to key parameters.

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