

Modeling forest stand dynamics from optimal balances of carbon and nitrogen

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Summary

- We formulate a dynamic evolutionary optimization problem to predict the optimal pattern by which carbon (C) and nitrogen (N) are co-allocated to fine-root, leaf, and wood production, with the objective of maximizing height growth rate, year by year, in an even-aged stand.
- Height growth is maximized with respect to two adaptive traits, leaf N concentration and the ratio of fine-root mass to sapwood cross-sectional area. Constraints on the optimization include pipe-model structure, the C cost of N acquisition, and agreement between the C and N balances. The latter is determined by two models of height growth rate, one derived from the C balance and the other from the N balance; agreement is defined by identical growth rates.
- Predicted time-courses of maximized height growth rate accord with general observations. Across an N gradient, higher N availability leads to greater N utilization and net primary productivity, larger trees, and greater stocks of leaf and live wood biomass, with declining gains as a result of saturation effects at high N availability. Fine-root biomass is greatest at intermediate N availability.
- Predicted leaf and fine-root stocks agree with data from coniferous stands across Finland. Optimal C-allocation patterns agree with published observations and model analyses.

Introduction

Strategies for investigating the interplay of carbon (C) and nitrogen (N) in plant growth include the evolutionary optimization and game paradigms (e.g. Mäkelä *et al.*, 2002). Optimization ordinarily involves the formulation of a teleonomic model to maximize an objective function with respect to one or more variable plant traits. The trait optimization is subject to physiological, structural, and environmental constraints on plant structure and function. In a game problem, the effect of competing individuals on the success of the alternative strategies is also considered (Maynard Smith, 1982; Mäkelä, 1985; King, 1993; Dybzinski *et al.*, 2011).

Examples of objective functions include net growth rate (Franklin, 2007), gross primary productivity (McMurtrie *et al.*, 2008), net energy for reproduction (Finnoff & Tschirhart, 2009), and total entropy production (Dewar, 2010). The optimization approach to modeling is efficient because it eliminates the need for explicit submodels of the variable traits and their attendant parameters (Dewar *et al.*, 2009). The prime justification for this modeling approach, however, is based on Darwinian selection: plants that are best at optimizing functional traits are the likeliest to survive to produce offspring. In this regard, the objective function serves as a proxy of fitness.

To date, applications of the evolutionary paradigm have provided testable predictions about the co-allocation of C and N to shoots and roots for either of the two extremes of plant growth, namely, exponential growth (Hilbert, 1990; Ågren & Franklin, 2003) or steady state (Dewar, 1996; Franklin, 2007; McMurtrie *et al.*, 2008; Mäkelä *et al.*, 2008; Dybzinski *et al.*, 2011). Models of exponential growth provide optimal patterns of co-allocation that maintain a balance between shoots and roots. The co-allocation satisfies demands for C and N that are defined by the fixed or plastic stoichiometries of the two tissues. The acquisition of C and N, respectively, is assumed to be proportional to shoot and root size (Johnson & Thornley, 1987; Mäkelä & Sievänen, 1987; Hilbert, 1990; Ågren & Franklin, 2003). Many of the optimal steady-state models focus on canopy properties when all available N is utilized, and therefore do not explicitly consider a C cost of N acquisition through the maintenance of a system of fine roots (e.g. Dewar, 1996; Franklin, 2007). However, a recent model by Mäkelä *et al.* (2008) generalized the idea of the exponential balanced-growth models to steady-state, resource-limited situations (see also Dybzinski *et al.*, 2011). Given the availability of soil N, this steady-state model maximizes net primary productivity (NPP) by optimizing the co-allocation of C and N to leaf and fine-root production, and to leaf N concentration. The optimal co-allocation is constrained

by: a structural model, that is, the pipe model (Shinozaki *et al.*, 1964); saturation levels of leaf and fine-root biomass with regard to C and N acquisition; and agreement between C and N balances. The steady-state model accounts for the C costs for producing and maintaining leaves, wood, and fine roots, and, in so doing, accounts for the cost of acquiring N by the root system.

The results of the balanced-growth optimization models, both exponential and steady state, are in reasonable agreement with our general understanding of how N availability influences C allocation. They suggest, for example, that increasing N availability reduces the allocation of C to fine roots while simultaneously increasing the leaf N concentration (Hilbert, 1990; Ågren & Franklin, 2003), and that the optimum steady-state stocks of leaves and fine roots are determined by the relative availabilities of C and N (Mäkelä *et al.*, 2008). The steady-state optimization model of Mäkelä *et al.* (2008) and the model of Dybzinski *et al.* (2011), which is based on evolutionarily stable strategies, indicate that the fraction of NPP allocated to leaf production in stands at steady state is largely unaffected by increasing N availability. The primary trade-off in allocation is between wood and fine-root production, the fraction of NPP allocated to wood increasing with N availability at the expense of fine roots. These model predictions are consistent with recent observations (Litton *et al.*, 2007). However, models differ in which adaptive traits are considered and the degree of plasticity allowed, particularly with regard to tissue N concentration.

To our knowledge, a dynamic analysis of optimal C and N co-allocation, bridging the early and later phases of stand growth, has not been reported (but see Franklin, 2007). A dynamic analysis of stand growth seems to require an explicit treatment of height growth, which, so far, has been ignored in most of the evolutionary optimization studies. In closed stands, trees compete for light and other resources, so rapid height growth is a crucial means of survival and reproductive success for species of low or moderate shade tolerance (e.g. Horn, 1971; Mäkelä, 1985). Key to a dynamic analysis is an understanding of how different resources influence shoot production and elongation so we can relate height growth to the material balances of the model. The optimization must account for the fact that the growth of shoots, coarse roots, and supporting stems involves a trade-off with the growth of the leaves and fine roots that capture the resources.

In this paper, we formulate a dynamic evolutionary optimization problem to predict the optimal pattern of co-allocation of C and N to the fine roots, leaves, and wood that maximizes height growth rate over the course of development of an even-aged stand. The analysis draws from our previous work on optimal C and N co-allocation in an even-aged, closed-canopy stand of trees at quasi steady state (Mäkelä *et al.*, 2008). Here we advance our previous approach with a height growth model derived from the requirements of C balance (Valentine & Mäkelä, 2005), the pipe model (Shinozaki *et al.*, 1964), and optimal crown allometry (Mäkelä & Sievänen, 1992). We also derive a second height growth model from the N balance in analogy to height growth rate based on the C balance. The two height growth rates are the same if the C and N balances are in agreement. In addition, we define the mortality rate of trees on the basis of leaf and fine-root

density, and assume that crown rise is driven by crowding in space (after Valentine *et al.*, 1994). Finally, we maximize the height growth rate of the trees by optimizing two adaptive traits – leaf N concentration and fine-root biomass per unit sapwood area – on a yearly time step. This strategy leads to optimizing photosynthetic N concentration and the co-allocation of C and N to the production of fine-root, leaf, and wood biomass, while accounting for the C costs of respiration and N acquisition from the soil.

The model is applied with parameter values appropriate for Scots pine (*Pinus sylvestris*) in southern Finland. We consider the dynamics of the co-allocation of N and C to fine roots, leaves, and wood in stands with different maximum rates at which N can be taken up from the soil. Because the focus of this paper is on growth dynamics, we ignore the N dynamics and assume that the abundance of available N within the soil at a given site is constant over time.

In order to assess the significance of some of the postulated constraints, we consider the implications of the degree of plasticity of the adaptive traits by comparing stand development patterns that emerge from optimal C and N balances against patterns that emerge from a law-of-the-minimum (LM) approach, that is, stand growth based on the minimum of the C or N-based height growth rates.

We bound our analysis by focusing on three research questions: first, to what degree do the values of the two adaptive parameters change over the course of stand development? Second, do the results under the law-of-the-minimum approach differ markedly from those under the optimal-balance approach? Finally, does a steady-state response represent the essence of the closed-canopy dynamics?

Description

The growth model is presented in sufficient detail for replication and advancement of our work.

Components of live biomass

We consider a pure stand of N (ha^{-1}) identical trees. Each tree has three components of live biomass (kg): W_l , leaves; W_r , fine roots; and W_w , sapwood. The total sapwood comprises the transport roots and aboveground sapwood. Leaves die and turn over after T_l years, and fine roots after T_r years. Sapwood volume is defined in terms of three state variables: A (m^2), the cross-sectional area of sapwood at the crown base ('sapwood area'); H (m), the height of the crown tip; and H_c (m), the height of the crown base.

Using a simple pipe model, we assume that the length of a strand of sapwood from a fine root to a leaf – the average length of an active pipe – is $H_c + \beta_c(H - H_c) + \beta_r(H - H_c)$, where $\beta_c(H - H_c)$ is the average length of pipe from the crown base to a leaf, and $\beta_r(H - H_c)$ is the average length of pipe below ground. Hence, average pipe length is $\beta_1 H + \beta_2 H_c$, where $\beta_1 = \beta_c + \beta_r$ and $\beta_2 = 1 - \beta_1$ are dimensionless parameters. The three live components of biomass, expressed in terms of the pipe model, are

$$W_f = \rho_f A \quad \text{Eqn 1}$$

$$W_r = \rho_r A \quad \text{Eqn 2}$$

$$W_w = \rho_w A(\beta_1 H + \beta_2 H_c) \quad \text{Eqn 3}$$

where ρ_f and ρ_r are ratios of biomass to sapwood area (kg m^{-2}). The parameter ρ_w is the bulk density of sapwood (kg m^{-3}). Hence the volume of sapwood is W_w/ρ_w .

Rates of change

Let dW_i/dt (kg yr^{-1}) be the rate of change of component $i = f, r, w$. Then, by definition,

$$\frac{dW_i}{dt} = G_i - S_i \quad \text{Eqn 4}$$

where G_i is the rate of production of new tissue, and S_i is the rate of loss of old tissue to senescence or deactivation. Similarly, the rate of change of sapwood area ($\text{m}^2 \text{yr}^{-1}$) is, by definition,

$$\frac{dA}{dt} = G_A - S_A \quad \text{Eqn 5}$$

where G_A is the rate of production of new sapwood area, and S_A is the rate of loss of old sapwood area to deactivation. Based on the optimal crown model of Mäkelä & Sievänen (1992) and the pipe model, Valentine & Mäkelä (2005) assumed that $A \propto (H - H_c)^z$, and decomposed the time derivative

$$\frac{dA}{dt} = \frac{zA}{H - H_c} \left(\frac{dH}{dt} - \frac{dH_c}{dt} \right) \quad \text{Eqn 6}$$

into

$$G_A = \left(\frac{zA}{H - H_c} \right) \frac{dH}{dt} \quad \text{Eqn 7}$$

$$S_A = \left(\frac{zA}{H - H_c} \right) \frac{dH_c}{dt} \quad \text{Eqn 8}$$

Note that subtraction of Eqn 8 from Eqn 7 gives Eqn 6. With the decomposition, the production rate of new sapwood is associated with the rate of height growth, and the deactivation rate of old sapwood is associated with the rate of crown rise, that is, the rate at which the crown base rises. This decomposition is key to the development of our model because with Eqns 7, 8, together with Eqns 1–3, we can express the rates of production of all three components of live biomass in terms of the dynamics of H and H_c , that is,

$$G_f = \left(\frac{zW_f}{H - H_c} \right) \frac{dH}{dt} + \frac{W_f}{T_f} \quad \text{Eqn 9}$$

$$G_r = \left(\frac{zW_r}{H - H_c} \right) \frac{dH}{dt} + \frac{W_r}{T_r} \quad \text{Eqn 10}$$

$$G_w = \left(\frac{zW_w}{H - H_c} + \frac{\beta_1 W_w}{\beta_1 H + \beta_2 H_c} \right) \frac{dH}{dt} \quad \text{Eqn 11}$$

The production rates of leaf and fine-root biomass, respectively, include annual rates of replacement of senescent leaf and fine-root biomass, W_f/T_f and W_r/T_r . The rates of growth and loss for all three components of biomass are provided in Supporting Information Notes S1.

Carbon-based model

The net primary productivity of the model stand is

$$\begin{aligned} \text{NPP} &= N(G_f + G_r + G_w) \\ &= Y(P - R_m) \end{aligned} \quad \text{Eqn 12}$$

where P and R_m , respectively, are the stand-level rates of photosynthesis and maintenance respiration ($\text{kg C ha}^{-1} \text{yr}^{-1}$) and Y ($\text{kg biomass (kg C)}^{-1}$) is the conversion efficiency of C to biomass, accounting for construction respiration (Thornley, 1970). Substitution of Eqns 9–11 into Eqn 12 provides the C-based rate of height growth (dH_{CB}/dt) as a function of P and R_m (Valentine & Mäkelä, 2005), that is,

$$\frac{dH_{CB}}{dt} = \frac{(Y(P - R_m)/N) - (W_f/T_f) - (W_r/T_r)}{[z \sum_i W_i/(H - H_c)] + [\beta_1 W_w/(\beta_1 H + \beta_2 H_c)]} \quad \text{Eqn 13}$$

($i = f, r, w$).

Following Mäkelä *et al.* (2008), we model P as a saturating function of leaf biomass

$$P = \sigma_{fM} W_f N \left(\frac{K_f}{K_f + W_f N} \right) \quad \text{Eqn 14}$$

where σ_{fM} ($\text{kg C (kg leaf)}^{-1} \text{yr}^{-1}$) is the light-saturated specific rate of photosynthesis, and K_f ($\text{kg ha}^{-1} \text{yr}^{-1}$) is the stand leaf biomass at which P equals half the saturated rate. We chose this model because its mathematical properties afford a closed-form solution at steady state. A formulation based on leaf area is an option, but would increase the number of parameters.

The specific rate, σ_{fM} , is modeled as a saturating function of the photosynthetic N concentration ($[N]_p$) (Field & Mooney, 1986; Hilbert, 1990; Ågren & Franklin, 2003; Ellsworth *et al.*, 2004), that is,

$$\sigma_{fM} = \sigma_{fM0} \left(\frac{[N]_p}{[N]_p + [N]_{ref}} \right) \quad \text{Eqn 15}$$

where σ_{fM0} ($\text{kg C (kg leaf)}^{-1} \text{yr}^{-1}$) is the N-saturated specific rate of photosynthesis, and $[N]_{ref}$ is the value of $[N]_p$ that provides half the N-saturated rate. $[N]_p$ is the difference between the total and structural leaf N concentration ($[N]_0$),

$$[N]_p = \max([N]_f - [N]_0, 0) \quad \text{Eqn 16}$$

The total leaf N concentration, $[N]_f$, changes with time because it is optimized from year to year. We assume that fine-root N concentration is proportional to $[N]_f$, that is, $[N]_r = r_N[N]_f$ (Helmisaari *et al.*, 2007).

We model the rate of maintenance respiration in terms of the component N concentrations (e.g. Ryan, 1991):

$$R_m = r_m N ([N]_f W_f + [N]_r W_r + [N]_w W_w) \quad \text{Eqn 17}$$

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

Nitrogen-based model

We assume that the rate at which N is concentrated in new biomass equals the rate of N uptake from the soil plus the rate of resorption of N from senescent biomass (kg N ha⁻¹ yr⁻¹), that is,

$$N ([N]_f G_f + [N]_r G_r + [N]_w G_w) = N_{\text{uptake}} + N_{\text{resorb}} \quad \text{Eqn 18}$$

Substituting Eqns 9–11 into Eqn 18, and solving for the N-based height growth rate (dH_{NB}/dt) yields

$$\frac{dH_{NB}}{dt} = \frac{[(N_{\text{uptake}} + N_{\text{resorb}})/N] - ([N]_f W_f/T_f) - ([N]_r W_r/T_r)}{[z \sum_i [N]_i W_i/(H - H_c)] + [\beta_1 [N]_w W_w/(\beta_1 H + \beta_2 H_c)]} \quad \text{Eqn 19}$$

($i = f, r, w$).

Analogous to our model of photosynthesis, Eqn 14, we model the rate of N uptake (kg N ha⁻¹ yr⁻¹) as a saturating function of W_r :

$$N_{\text{uptake}} = \sigma_{rM} W_r N \left(\frac{K_r}{K_r + W_r N} \right) \quad \text{Eqn 20}$$

where σ_{rM} (kg N (kg fine root)⁻¹ yr⁻¹) is the maximum fine-root specific rate of N uptake, and K_r (kg ha⁻¹) is the stand fine-root biomass at which the N uptake rate equals half the maximum rate.

As leaf biomass turns over, a fraction of its N content is resorbed for reuse in production. It seems plausible that resorption also may occur as fine roots turn over. Let f_f and f_r , respectively, be resorption fractions from senescent leaves and fine roots; then

$$N_{\text{resorb}} = N \left(\frac{f_f [N]_f W_f}{T_f} + \frac{f_r [N]_r W_r}{T_r} \right) \quad \text{Eqn 21}$$

Hydraulic limitation

Hydraulic resistance to sap flow reduces the specific rate of photosynthesis, σ_{fM} , in some species (Yoder *et al.*, 1994). As the greatest resistance occurs in branches (Hellkvist *et al.*, 1974; Tyree, 1988), we follow Mäkelä (1997), and account for the resistance effect by letting σ_{fM} decrease with crown length, that is,

$$\sigma_{fM, \text{lim}} = \sigma_{fM} [1 - a_\sigma (H - H_c)] \quad \text{Eqn 22}$$

We assume a proportional decrease in the maximum fine-root specific rate of N uptake:

$$\sigma_{rM, \text{lim}} = \sigma_{rM} \left(\frac{\sigma_{fM, \text{lim}}}{\sigma_{fM}} \right) \quad \text{Eqn 23}$$

Stand density and spacing

By definition, average tree spacing, X (m), depends on the stand density, N (ha⁻¹), that is, $X \equiv 100/\sqrt{N}$. Consequently, the rate of increase in the average spacing (m yr⁻¹) attributable to tree mortality (ha⁻¹ yr⁻¹) is:

$$\frac{dX}{dt} = -\frac{50}{N^{3/2}} \frac{dN}{dt} \quad \text{Eqn 24}$$

We assume that tree mortality begins when either leaf or fine-root biomass per unit land area reaches a critical value. We define the rate of mortality with parameters of the saturating photosynthesis and N uptake functions. Hence, the mortality rate, M_i (ha⁻¹ yr⁻¹), triggered by leaf ($i = f$) or fine-root ($i = r$) abundance, is

$$M_i = \begin{cases} 0, & W_i N < \frac{K_i}{2} \\ \left(\frac{m_i W_i N}{K_i} \right) N, & \text{otherwise} \end{cases} \quad \text{Eqn 25}$$

where m_i (yr⁻¹) is a rate parameter. The actual mortality rate is the maximum of M_f and M_r , that is,

$$\frac{dN}{dt} = -\max\{M_f, M_r\} \quad \text{Eqn 26}$$

Crown rise

The rate of crown rise is based on the model of Valentine *et al.* (1994), which posits that average crown length in a closed stand is proportional to the average spacing among trees, that is, $H - H_c = \beta_3 X$. A model stand is deemed open if $H < \beta_3 X + H_c$. Hence, crown rise begins (or resumes) as $H \rightarrow \beta_3 X + H_c$; therefore,

$$\frac{dH_c}{dt} = \begin{cases} 0, & H < \beta_3 X + H_c \\ \frac{dH}{dt} - \beta_3 \frac{dX}{dt}, & \text{otherwise} \end{cases} \quad \text{Eqn 27}$$

In concert with observations from fertilizer trials of loblolly pine (*Pinus taeda*) (Albaugh *et al.*, 2006), we assume that longer crowns are supported by greater fertility. We achieve this effect by letting β_3 vary with the leaf-specific rate of photosynthesis, that is,

$$\beta_3 = \beta_{30} + \beta_{31} \sigma_{fM, \text{lim}} \quad \text{Eqn 28}$$

Model solution

The model is organized as an initial value problem and solved, year by year, by numerical integration. Starting values for the

solutions presented here are $A = 0.284 \times 10^{-5} \text{ m}^2$, $H = 0.1 \text{ m}$, and $H_c = 0 \text{ m}$. The initial stand density is $N = 1600 \text{ trees (ha}^{-1}\text{)}$ for most scenarios. Eqns 1–3 provide the initial values of the components of biomass. Parameter values are provided in Table 1. (Note: the resorption fraction, f_r , is fixed at 0 because N cycling is ignored, and the availability of soil N is assumed constant.)

We assume that each of the N identical ‘model trees’ in a stand is endowed with two adaptive traits: the ratio of fine-root biomass to sapwood area, ρ_r , and the leaf N concentration, $[N]_f$. The values of these two free parameters must satisfy the balanced growth constraint, that is, $dH_{CB}/dt - dH_{NB}/dt = 0$. To achieve this, we express the right-hand sides of the two rate equations, Eqns 13, 19, in terms of the pipe model as factors of ρ_r , which provides

$$\frac{dH_{CB}}{dt} - \frac{dH_{NB}}{dt} = \rho_r^3 + a_1 \rho_r^2 + a_2 \rho_r + a_3 = 0 \quad \text{Eqn 29}$$

where a_1 , a_2 , and a_3 are functions of the state variables and parameters, including $[N]_f$ (Notes S2). Thus, Eqn 29 provides the value(s) of ρ_r for which $dH_{CB}/dt = dH_{NB}/dt$ given any proposed value of $[N]_f$ and, therefore, any set of trait values comprising the proposed value of $[N]_f$ and the calculated value of ρ_r ensures balanced growth. Of interest is the optimal set of values that maximizes dH_{CB}/dt (or minimizes $-dH_{CB}/dt$). We used numerical

search or the Nelder–Mead simplex method (see, e.g. Press *et al.*, 2003) to find the optimal sets.

In our solutions, we re-optimized the values of the free parameters at the start of each year, and used those values for the duration of that year. By re-optimizing these trait values, we effectively optimized the co-allocation of C and N to the production of the three components of biomass: W_f , W_r , and W_w .

The model also can be solved without year-to-year optimization by assigning fixed values to free parameters. Or, given the maximum rate of N uptake, we can search for the optimal fixed values of $[N]_f$ and ρ_r that maximize total tree height at a reference age of, say, 50 yr. As fixed parameters do not change year to year, equality of C-based and N-based height growth rates over any lengthy period of time is unlikely. Therefore, we solve the model using an LM approach, that is, height growth rate equals the slower of the C-based or N-based growth rates:

$$\frac{dH}{dt} = \min \left\{ \frac{dH_{CB}}{dt}, \frac{dH_{NB}}{dt} \right\} \quad \text{Eqn 30}$$

Results

Because the model can be solved in two ways, we call solutions with adaptive traits and optimal C and N balances the optimal balance (OB) approach, and solutions with fixed traits the LM approach.

Table 1 Parameter symbols, definitions, values, and units

Symbol	Definition	Value	Units
a_σ	Reduction in leaf-specific rate of photosynthesis per unit crown length (hydraulic limitation)	0.02	kg C m ⁻¹
f_f	N resorption fraction from senescent leaves	0.0	–
f_r	N resorption fraction from senescent fine roots	0.0	–
K_f	Leaf biomass for half maximal photosynthesis	3500.0	kg ha ⁻¹
K_r	Fine-root biomass for half maximal N uptake	3500.0	kg ha ⁻¹
m_f	Mortality rate from aboveground forcing	0.007	yr ⁻¹
m_r	Mortality rate from belowground forcing	0.014	yr ⁻¹
$[N]_0$	Non photosynthetic N concentration in leaves	9.5	mg g ⁻¹
$[N]_f$	Total N concentration in leaves	Optimal	mg g ⁻¹
$[N]_{ref}$	N concentration in leaves for half maximal leaf-specific rate of photosynthesis	1.0	mg g ⁻¹
$[N]_w$	N concentration in sapwood	0.7	mg g ⁻¹
r_N	Ratio of fine-root to leaf N concentration	0.6	–
r_m	N specific rate of maintenance respiration	24.0	kg C kg ⁻¹ yr ⁻¹
T_f	Leaf longevity	3.33	yr
T_r	Fine-root longevity	1.25	yr
Y	Conversion ratio of C to biomass	1.54	kg (kg C) ⁻¹
z	Scaling exponent: $A \propto (H - H_c)^z$	1.86	–
β_c	Ratio of average pipe length above the crown base to crown length	0.77	–
β_r	Ratio of average pipe length below ground to crown length	0.50	–
β_{3_0}	Baseline value of β_3 , the ratio of crown length to tree spacing after closure	1.1	–
β_{3_1}	Slope of β_3 vs leaf-specific rate of photosynthesis	0.30	g mg ⁻¹
ρ_f	Ratio of leaf biomass to sapwood area	460.0	kg m ⁻²
ρ_r	Ratio of fine-root biomass to sapwood area	Optimal	kg m ⁻²
ρ_w	Ratio of sapwood biomass to sapwood volume	400.0	kg m ⁻³
σ_{fM0}	N-saturated leaf-specific rate of photosynthesis	6.0	kg C (kg leaf) ⁻¹ yr ⁻¹

We solved the model for six different initial stand densities: 800, 1200, ..., 2800 (trees ha^{-1}), by six different maximum N uptake rates: $N_{\text{up,max}} = 40, 60, \dots, 140 \text{ kg N ha}^{-1} \text{ yr}^{-1}$. As it turned out, altering the initial stand density has only a minor effect on the behavior of the model so we concentrate on results for six different maximum uptake rates given an initial stand density of 1600 trees ha^{-1} . We do, however, provide some results for the six initial stand densities, given a maximum N uptake rate of $100 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Notes S3, Fig. S3).

Plasticity of traits and model stand behavior

With the OB approach, variation in the availability of N leads to wide variation in the two adaptive traits, leaf N concentration, $[N]_f$, and the ratio of fine-root mass to sapwood area, ρ_r , the predicted optimal values of former increasing, and the latter decreasing, with increasing values of $N_{\text{up,max}}$ (Fig. 1a,b). Because these traits are optimized from year to year, they also show plasticity over time (Fig. 1c,d). The temporal plasticity is more pronounced in the values of ρ_r , which are greatest at stand initiation, decreasing to approach their respective, nearly constant, final values at stand closure. The ratio of leaf mass to sapwood area, ρ_f , is fixed at 460 kg m^{-2} , so the ratio $\rho_r : \rho_f$ initially exceeds 1 for every value of $N_{\text{up,max}}$, meaning that fine-root mass initially exceeds leaf mass in every case.

The OB approach gives rise to a wide array of dynamics (see Notes S3, Figs S1–S3). The predicted time-courses of gross primary productivity (GPP), NPP, and the percentages of NPP allocated to the three components of biomass are depicted in Fig. 2. GPP increases rapidly after initiation and then tends to plateau or gradually decline by a small amount after closure (Fig. 2a). NPP, by contrast, tends to decline more rapidly after

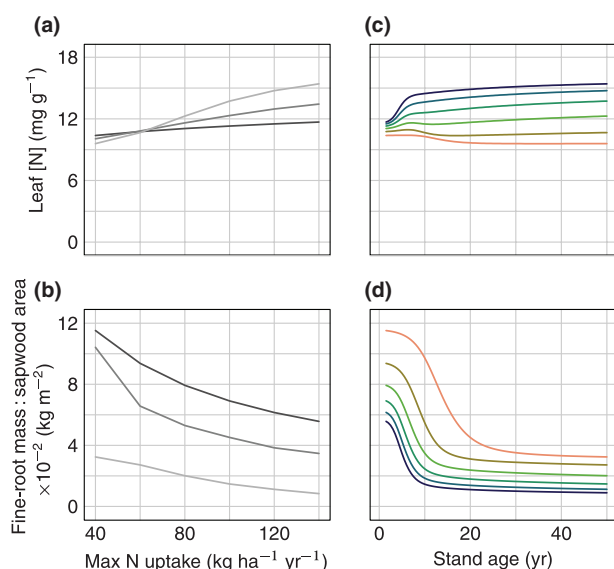


Fig. 1 Left: (a) Predicted leaf nitrogen (N) concentration ($[N]_f$) and (b) the ratio of fine-root mass to sapwood area (ρ_r) vs maximum N uptake rate (dark, stand initiation; medium, time of peak height growth; light, stand age 50 yr). Right: (c) $[N]_f$ and (d) ρ_r vs stand age for six maximum N uptake rates: 40 (red), 60 (gold), 80 (green), 100 (dark green), 120 (blue), 140 (dark blue) $\text{kg N ha}^{-1} \text{ yr}^{-1}$.

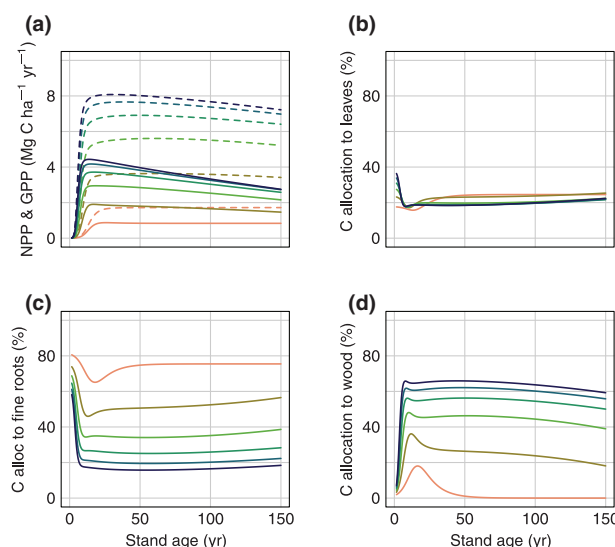


Fig. 2 Predicted time-courses by maximum nitrogen (N) uptake rate of 40 (red), 60 (gold), 80 (green), 100 (dark green), 120 (blue), 140 (dark blue) $\text{kg N ha}^{-1} \text{ yr}^{-1}$: GPP (dashed line) and NPP (a), and the percentage of NPP allocated to (b) leaves; (c) fine roots; and (d) sapwood. GPP and NPP, respectively, are gross and net primary productivity.

peaking, except at the lowest levels of N uptake. The ratio of net to gross primary productivity declines over the course of stand development from about 0.72, initially, to about 0.4 at 150 yr, with some variation, the N-poor stands having the larger final ratios (not shown).

The predicted fraction of NPP allocated to leaf (Fig. 2b) and fine-root production (Fig. 2c) decreases between stand initiation and closure. An initially large fraction of NPP allocated to leaf biomass decreases rapidly before the stand closes, and then the fraction tends to stabilize at about 0.2 (or 0.25 at the lowest levels of N uptake) with a slight increase as the stand ages. An obvious trade-off in C allocation between fine-root and sapwood production is evident in Fig. 2(c,d). At any given point in time, less C allocation to fine roots is matched by more C allocation to wood, and vice versa. Fine-root production decreases, and wood production increases, with increasing N availability. N saturation effects are apparent at the higher values of $N_{\text{up,max}}$ with regard to GPP, NPP, and the allocation of NPP to fine roots and wood.

Predicted time-courses of the components of biomass and total N in biomass are provided in Fig. 3. Greater N content (Fig. 3a) is associated with greater sapwood mass (Fig. 3b), and leaf mass (Fig. 3c). After closure, fine-root mass is greatest for intermediate N uptake rates (Fig. 3f), which accords with the steady-state model of Mäkelä *et al.* (2008). N saturation effects at the higher rates of N uptake are evident for all the traits except fine-root mass.

Optimal vs limited growth

The optimum time-course of the objective function, height growth rate, behaves realistically, increasing from stand initiation and peaking before closure, and then declining as the model stand ages (Fig. 4a). The time integral of this rate provides the expected sigmoid time-course of average tree height (Fig. 4c).

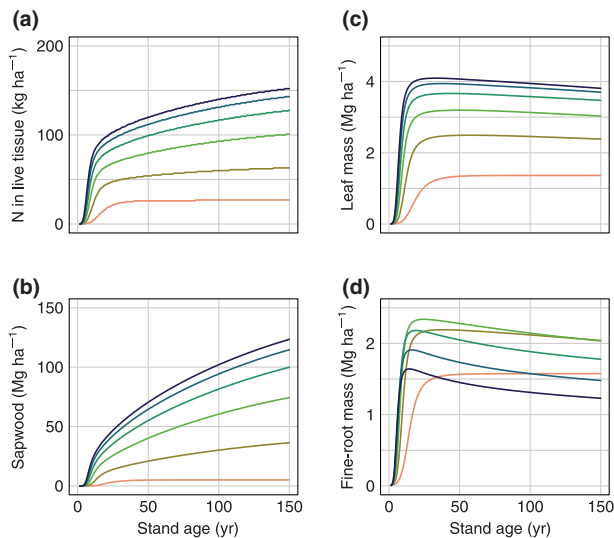


Fig. 3 Predicted nitrogen (N) content and biomass stocks, by maximum N uptake rate of 40 (red), 60 (gold), 80 (green), 100 (dark green), 120 (blue), 140 (dark blue) $\text{kg N ha}^{-1} \text{yr}^{-1}$: (a) total N in live biomass; (b) sapwood biomass; (c) leaf biomass; and (d) fine-root biomass.

For the LM approach (Fig 4b,c), fixed values of $[N]_f$ and ρ_r were optimized to maximize total tree height at age 50 yr, given the maximum rate of N uptake, $N_{\text{up,max}}$. Thus, the LM solutions for each value of $N_{\text{up,max}}$ are based on a unique set of fixed trait values.

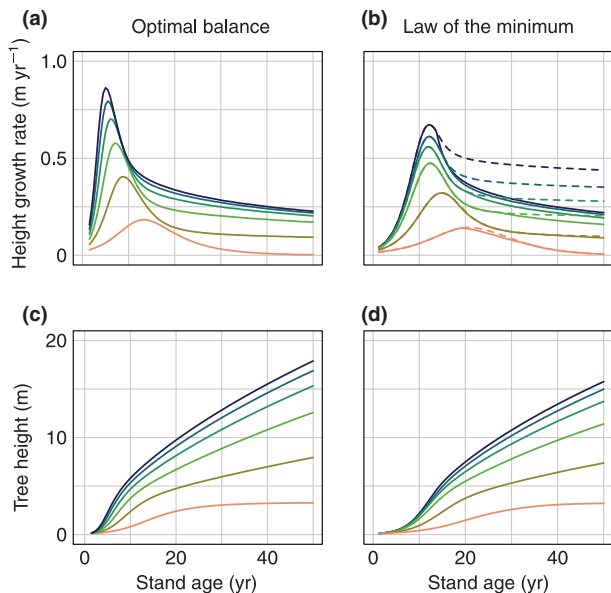


Fig. 4 Predicted time-courses from optimal-balance (left) or law-of-the-minimum solutions (right): (a, b) height growth rate; (c, d) average tree height. Colors are keyed to final tree heights (b), which increase with maximum nitrogen (N) uptake rate: 40 (red), 60 (gold), 80 (green), 100 (dark green), 120 (blue), 140 (dark blue) $\text{kg N ha}^{-1} \text{yr}^{-1}$. The law-of-the-minimum results are based on fixed values of leaf N concentration ($[N]_f$) and the ratio of fine-root mass to sapwood area (ρ_r) that maximize tree height at age 50 yr. Solid lines in (b) are the law-of-the-minimum growth rates, and dashed lines are the N-based solutions (N-based growth rates are smaller initially, then C-based growth rates are smaller after closure for the four highest rates of N uptake).

Compared with the LM approach, stands modeled under the OB approach achieve closure faster and yield taller average tree heights at any given age, and for any given value of $N_{\text{up,max}}$. Decreasing differences between tree heights for the faster maximum rates of N uptake indicate a tendency toward N saturation. Note that, even with this tendency, the height growth rates under the LM approach initially are limited by N uptake (Fig. 4b). N limitation persists after closure at the two slowest rates of N uptake, but C becomes limiting to growth after closure at the four faster rates. By comparison (Fig. 4c,d), the two approaches to optimization do not yield markedly different results, but it is clear that maintaining optimal C and N balances – which presumes plasticity in tree structure and function with regard to the acquisition of C and N – is the more beneficial life style if rapid height growth promotes survival.

Leaf N concentrations are similar under the two optimization approaches, and the post-closure values of ρ_r for the OB approach are very similar to the fixed LM values for corresponding N uptake rates (Fig. S4). This seems to suggest that OB trees gain much of their advantage over LM trees early in life. But that is because the fixed parameters of the LM trees maximize tree height at age 50 yr. Were we to choose fixed parameter values to maximize tree height at, say, age 10 yr, then the OB trees would seem to gain more of their advantage later in life (Notes S4, Fig. S5).

Dynamic vs steady state

To address the question of whether a steady-state model can capture the essence of certain traits after closure, we compared solutions of the OB model at ages 50, 100, and 150 yr, over a range of N availability. We quantified N availability as the asymptotic fine-root-specific rate of N uptake, $\sigma_{\text{rM}} = N_{\text{up,max}}/K_r$. This result is obtained from Eqn 20 with $NW_r \rightarrow \infty$.

Fig. 5 depicts three predicted trend lines for particular traits vs N availability, one line for each age. Coincidence of the three trend lines would indicate a steady state over the 100-yr period. That trend lines are proximal, but not coincident, suggests that steady-state solutions do not apply exactly, but may apply approximately over one or more decades. The steady-state approximation applies better to leaf biomass and GPP (Fig. 5a,c) than to fine-root biomass, NPP, or leaf N concentration.

Some traits, such as height and stemwood biomass, increase continuously, and therefore are ignored in steady-state models. However, the fractions of NPP allocated to the three components of live biomass, including sapwood biomass, do tend to approach steady states (Fig. 5d). A hint of a trade-off in C allocation between sapwood and leaf production is seen at the lowest levels of N availability, but a pronounced trade-off is evident between fine-root and sapwood production, with increasing allocation to sapwood, and decreasing allocation to fine roots, with increasing N availability. These results are nearly identical to those reported by Mäkelä *et al.* (2008).

Field estimates of leaf and fine-root biomass, and leaf [N] were obtained for eight stands dominated by Scots pine across a climatic gradient in Finland (Helmisaari *et al.*, 2007). The stands

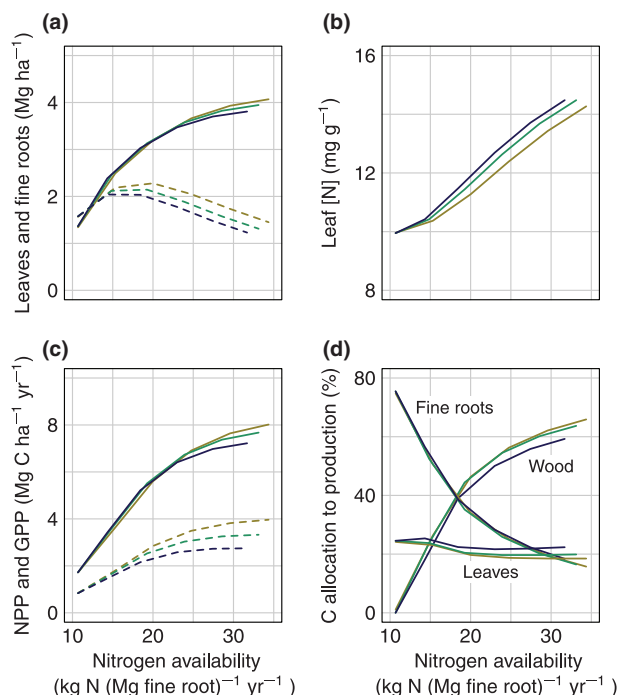


Fig. 5 Optimal model solutions over a range of nitrogen (N) availability at 50 (gold), 100 (green), and 150 (blue) yr: (a) leaf (solid) and fine-root (dashed) biomass; (b) leaf N concentration; (c) gross (solid) and net (dashed) primary productivity; (d) C allocation to production of fine roots, leaves, and wood.

occur on different site types with different stages of development, and they were all situated in the Boreal zone, where the effective temperature sum varies between 660 and 1290 degree-days per year. A summary of the data can be found in the supporting information for Mäkelä *et al.* (2008). There was considerable scatter in the estimates for both leaf and fine-root biomass vs $[N]_f$, but the present model suggests that some of this scatter could be attributable to factors associated with stand age and tree density – inasmuch as the elevations of the trend lines from the model solutions decrease with age and increase with density (Fig. 6a,b). Regardless of which factors are at play, the order of magnitude and general patterns of the model solutions over a range of N availability are consistent with the field estimates. Interestingly, all the trend lines from the present OB model for the leaf to fine-root ratio are nearly coincident, and show reasonable agreement with both the steady-state model of Mäkelä *et al.* (2008) and the field estimates (Fig. 6c).

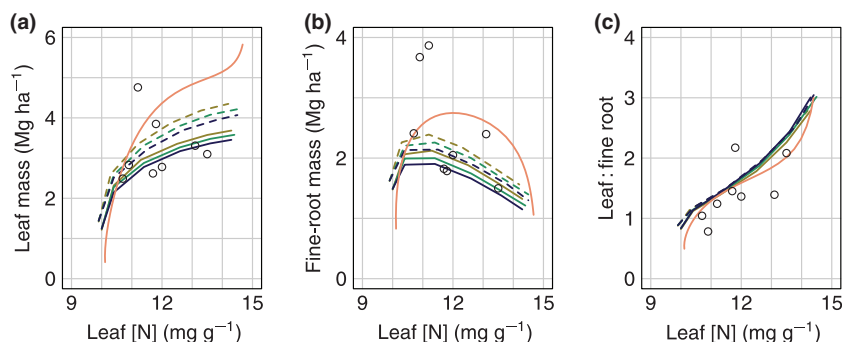


Fig. 6 Sample-based estimates (○) from Finnish stands of Scots pine for (a) leaf mass, (b) fine-root mass, and (c) the ratio of leaf to fine-root mass vs leaf $[N]$. The lines are optimal model solutions at 50 (gold), 100 (green), and 150 (blue) yr with initial stand densities of 800 (solid) or 2800 (dashed) trees ha^{-1} . Results from the steady-state model of Mäkelä *et al.* (2008) are shown in red.

Discussion

Plasticity of traits and model stand behavior

A major rationale for applying evolutionary optimization to models of plant function is the need to understand the life strategies of plants in terms of the plasticity of environmentally adaptive or acclimative traits. In this respect, the present model is consistent with previous work (Hilbert, 1990; Dewar, 1996; Ågren & Franklin, 2003; Franklin, 2007; McMurtrie *et al.*, 2008; Mäkelä *et al.*, 2008; Dybzinski *et al.*, 2011) and our general understanding of plant responses to variations in N availability. For example, the C fraction allocated to leaf production after closure is near the 20% value reported by Litton *et al.* (2007) for most forests (Fig. 2b). The remaining C allocation is, therefore, a trade-off between fine roots and sapwood (Figs 2c,d, 5d). The predicted total fine-root biomass in a mature stand is lowest where N is either least or most available. Fine-root biomass is highest where N availability is mid-range, in agreement with field data. This complex behavior of predicted fine-root biomass with regard to stand age and N availability is an emergent property of the optimization.

The predictions of the degree of plasticity in the adaptive traits, from stand initiation onwards, are new results. Few data are available for direct comparisons with these predictions, though other researchers have assumed that fine-root allocation is greater in the early phase of stand development (Running & Gower, 1991; Bossel, 1996).

To formulate the present model, we simplified features of stand development in many ways, focusing on what we considered essential. That we, like Dybzinski *et al.* (2011), ignored the dynamics of N cycling in the soil may be important concerning the temporal patterns of the adaptive traits. Explicit N cycling might change the solution to some extent, especially under nutrient-limited conditions, or where considerable N is bound within accumulations of litter and humus. However, we may have partly compensated for these conditions by our assumption of no N resorption from senescent leaves – at least that was our intent. Inasmuch as our optimization method would lend itself equally well to situations where the availability of nutrients varies with time, inclusion of an N cycling model is a logical next step for advancement of the model.

In this study, we limited our consideration of plasticity to two traits. We did not optimize plasticity of crown shape or foliar

density in the crown, although we did include an impact of N availability on crown length. Plasticity of crown shape has implications regarding the acclimation of trees to different canopy layers and, hence, to competition between individuals in the stand (see Horn, 1971; Oliver & Larson, 1990). Considering competition from the evolutionary point of view would require that we define the problem as a dynamic game so that the competitive interactions could be considered explicitly (see, e.g. Mäkelä, 1985). Because we optimized height growth directly, allowance for plasticity in crown shape would have rendered the problem ill-defined, as a narrower or sparser crown would always lead to faster height growth in the short term. However, several studies suggest that the architecture of tree structure is an evolutionary optimization problem that is somewhat independent of growth rate (see Horn, 1971; Mäkelä & Sievänen, 1992; West *et al.*, 1999; Duursma *et al.*, 2010), supporting the idea of separating the treatment of the two problems.

Many studies have considered the plasticity of N content and the consequent variability of photosynthetic capacity inside the canopy. For example, Hollinger (1996) demonstrated that trees allocate N to leaves in a nearly optimal way, with greater N concentrations per unit leaf area where photons are abundant, and lower concentrations where photons are sparse. On the basis of leaf mass, however, the N concentrations did not vary significantly, that is, N mass per unit leaf mass was roughly uniform throughout the crown. The two observations conform with each other if we interpret the leaf area per unit mass as a simple physical response to the light environment. To wit, leaves stretch their masses over larger areas in the shaded parts of the canopy, decreasing the N mass to leaf area ratio, while keeping the N mass to leaf mass roughly constant. This means that, when considering both the rate of photosynthesis and the N concentration in leaves on a mass basis, as was done in this study, the within-canopy variation of photosynthesis can be regarded solely as a function of light availability.

Optimal vs limited growth

Several models have assumed that the dynamic co-allocation of N and C is based on a combination of balanced growth and N limitation (Running & Gower, 1991; Bossel, 1996; Landsberg & Waring, 1997). The balanced growth hypothesis implies that more fine roots are required relative to leaves in N-poor sites, while the N limitation leads to reduced growth when the available N is insufficient to support the amount of production implied by the availability of C. These approaches leave open questions concerning the transfer from the early balanced growth to presumed N limitation as the trees grow larger: How much growth is allocated to fine roots if N is limited, that is, what amount of fine-root mass is sufficient to harvest the available N? How does tissue N concentration and, hence, the N demand of production vary with N availability? How do variations in tissue N concentration affect the physiological rates related to C and N acquisition? Heuristic assumptions (Running & Gower, 1991), empirical observation (Landsberg & Waring, 1997), and detailed mechanistic models (Bossel, 1996) have been explored to suggest

answers to these questions for purposes of predicting the dynamic response of growth to N availability.

By modeling stand growth with optimal balances, however, these questions become moot, as the overarching assumption is that, through plasticity of key traits, the trees adjust structure and function to optimize the use of available resources. Relaxing this overarching assumption, and taking an LM approach with the present model (fixing $[N]_f$ and ρ_r to maximize tree height at a reference age) produced an interesting result: N was limiting initially at all levels of N availability, but a switch to C limitation occurred at closure where N availability was moderate to high (Fig. 4b). That C may be limiting after closure may explain, to some degree, the popularity and success of C-balance models for modeling forest growth.

Modeling stand growth using the concept of limiting factors, rather than achieving agreement between the N and C balances, may yield good results and insights (e.g. Dybzinski *et al.*, 2011). The time-courses of height for the OB and LM approaches from the present model are very similar (Fig. 4a,d), although greater tree heights, at a given point in time, are achieved with optimal balances of C and N. Nonetheless, if the traits crucial for achieving the optimal balances lack sufficient plasticity, then the LM solution may be closest to the truth. As a consequence, however, the excess element might be wasted, for example, through an increased rate of respiration (Dewar, 2001), or by a release of sugars as root exudates (Hari & Kulmala, 2008). In this regard, growth based on agreement between the C and N balances is more efficient, and, we conjecture, more likely from a Darwinian standpoint. We further conjecture that if a model indicates that it is less profitable to achieve agreement between the N and C balances than to waste resources, then it is likely that the model lacks the mechanism to achieve profitable agreement. However, if optimal results suggest wider plasticity than has been observed, then it is likely that additional constraints are at play, which have not been considered.

Dynamic vs steady state

Our primary objective for this study was to extend the steady-state model of Mäkelä *et al.* (2008) to a dynamic situation to provide insights into the dynamics of N and C co-allocation and its implications for whole-stand dynamics, and also test the generality of the steady-state model. In accordance with both goals, we formulated the dynamic model to be as consistent as possible with the steady-state model. The key differences were the inclusion of height growth, crown rise, and mortality. Importantly, the objective function was chosen to be the maximization of height growth rate instead of NPP.

As already noted, previous evolutionary optimization studies have used a range of objective functions, chosen appropriately for the problem at hand. In the steady-state model, our objective function was NPP. We could not use height growth as the objective function because, by definition, there is no growth at steady state, as production equals senescence. However, we allowed the steady-state height to increase with increasing N availability. For the dynamic model, we assumed that rapid height growth is a trait of most low to moderately shade-tolerant trees that survive

self-thinning. It has been shown earlier that maximization of height growth is an evolutionarily stable strategy for trees competing for light (Mäkelä, 1985; King, 1993), and that this strategy does not necessarily maximize proxies of stand-level fitness, such as NPP (Maynard Smith, 1982).

Despite the differences, the results indicate qualitative agreement between the two models, where such agreement can be expected. This applies to the growth allocation patterns as well as the trends in biomass components with increasing N availability (Figs 2, 5) (see Mäkelä *et al.*, 2008). We conclude that these results essentially rely on our assumptions concerning tree structure, that is, the pipe model, and our assumptions regarding N and C acquisition, which were shared by both the static and the dynamic approaches. In the dynamic approach, we explicitly connected height growth with the N and C balance of the tree, resulting in a dependence between maximum height growth and N availability. In the static approach, a similar pattern was obtained by maximizing NPP at steady state while demanding that the stable height increase with N availability. These results suggest that optimization problems may be simplified with appropriate choices of constraints and objectives, although it is difficult to provide any general rule for guiding such choices.

Conclusions

In conclusion, this study concerned the optimal co-allocation of C and N in pure, even-aged stands with the objective of maximizing height growth rate. This means that the primary field of application of the results is among species that naturally form single-cohort stands, for example, through fire-controlled regeneration patterns. Particularly, this would cover several species of pine, as well as other shade-intolerant conifers. However, as height growth is crucial for the survival of most species in approximately even-aged populations, it seems likely that similar selective pressures also have prevailed for a wide range of species. Moreover, the model and the related optimization method, which allows for temporally varying traits, also would be applicable to the analysis of the possible optimal responses of trees to silvicultural treatments, for example, harvests or fertilization. The results of this study can be regarded as hypotheses concerning growth patterns and traits that should be more thoroughly tested against empirical data in future research.

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Supporting Information

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

Fig. S1 Predicted time-courses of nitrogen availability and utilization.

Fig. S2 Predicted time-courses of forestry inventory variables.

Fig. S3 Effects of initial stand density.

Fig. S4 Predicted time-courses of the adaptive traits.

Fig. S5 Predicted time-courses from optimal balance and law-of-the-minimum solutions.

Notes S1 Rates of growth, production, and loss.

Notes S2 Derivation of the optimal balance constraint, Eqn 29.

Notes S3 Additional results from the optimal balance solutions.

Notes S4 Comparison of optimal balance and law-of-the-minimum solutions.

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