Modeling forest growth
II. Biomass partitioning in Scots pine

Eberhard O. Voit a, Peter J. Sands b,*

a Department of Biometry and Epidemiology, Medical University of South Carolina, Charleston, SC 29425-2503, USA
b Cooperative Research Centre for Temperate Hardwood Forestry and CSIRO Division of Forestry, Locked Bag 2, Sandy Bay, Tasmania 7005, Australia

Received 13 June 1994; accepted 23 November 1994

Abstract

Biomass budgets of Scots pine (Pinus sylvestris) are analyzed with a canonical S-system model. The model is constructed with standardized methods of power-law representation, and a complete set of parameter values is derived from experimentally measured compartment sizes, fluxes and nitrogen contents. None of the typical assumptions about growth rates, relationships between roots and shoots, or allometry are made. All these phenomena are produced by the model as outputs. Specifically, the model correctly predicts the different long-term growth patterns of leaves, stems, and roots; relationships between these compartments, biomass production, and growth rates; and relationships that constitute the concept of functional balance. The model also predicts allocation patterns for biomass under different fertilization regimens and during the ageing of a stand. These latter predictions are more complicated than expected but appear reasonable, though definitive data for validation are lacking.

Keywords: Growth; Partitioning; Pinus sylvestris; S-system models; SWECON Project

1. Introduction

Forests are the paradigm of organizationally complex systems. Trees have lifetimes of several decades, and yet their life depends on biochemical and physiological processes that proceed at the time scale of seconds. Wood production is measured in tons per hectare, and yet this production is driven by energy that is managed in mitochondria with sizes in the micrometer range. These wide ranges in size and time scales make any modeling effort complicated. Biochemical and physiological models, focussing on a low level of organization, become overwhelmingly complicated at the scales of entire trees or tree stands, while growth and yield models, focussing on trees as individuals, have no explanatory power when it comes to questions of how and why a tree is growing at all.

Since growth, yield, and biomass allocation can be altered artificially through fertilization and irrigation, a better quantitative understanding of the allocation or partitioning processes in tree stands is of great importance for the management
and optimization of wood production and quality. The relevance of biomass partitioning is reflected in a comprehensive body of literature which has been reviewed in general (e.g., Cannell, 1985; Dickson, 1989; Wardlaw, 1990; Farrar, 1992) or with special emphasis on mathematical models (e.g., Wilson, 1988; Gillespie and Chaney, 1989; Mäkelä, 1990; Thornley and Johnson, 1990). While the difficulties in understanding forest dynamics are commonly realized, there is no doubt that it is highly desirable to develop quantitative methodologies for evaluating the growth and yield dynamics of forests.

In the preceding paper (Volt and Sands, 1996), we described a canonical approach to modeling organizationally complex systems in which variables differ by several orders of magnitude and processes occur at vastly different time scales. We discussed similarities and differences between the canonical and the process-based modeling approaches and indicated in which situations the canonical approach might be particularly useful. In this paper, we show how the canonical modeling approach can be applied to biomass partitioning and analyze data on Scots pine (Pinus sylvestris).

The proposed approach is based on rigorous approximation theory and defines compartments and overall fluxes into and out of these compartments as the focus of analysis. It uses qualitative knowledge about the phenomenon of interest but requires no assumptions about physiological mechanisms or parameter values. The resulting model is mechanistic in a sense that each term uniquely represents a specific flux process and each variable and each parameter has a clearly defined meaning, even though the meaning of some components may appear obscure at first. At the same time, the model may be reminiscent of empirical models, since components of its mathematical structure are known in a slightly simpler form from growth and yield models (e.g., Clutter et al., 1983), and since the estimation of parameters uses statistical regression with whole tree data rather than detailed experimental measurements of individual biochemical mechanisms or transport processes.

Since the modeling techniques were described in the companion paper (Volt and Sands, 1996), this paper is primarily concerned with the description of data, estimation of model parameters, and results on growth trends and patterns of biomass partitioning.

2. Data

The data represent three plantations of Scots pine (Pinus sylvestris) that were part of the

| Variable | $t = 14$ | $t = 20$ (N-) | $t = 20$ (N+)
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>obs</td>
<td>model</td>
<td>obs</td>
</tr>
</tbody>
</table>
| Compartment sizes
| $X_1$    | (0.02)   | 0.022        | (0.06)       | 0.054        | (0.12) | 0.184    |
| $X_2$    | 1.23     | 1.26         | 4.17         | 4.57         | 10.59  | 10.80    |
| $X_3$    | 1.88     | 1.89         | 9.67         | 9.83         | 26.12  | 25.60    |
| $X_4$    | 0.80     | 0.76         | 3.12         | 3.22         | 6.45   | 6.22     |
| Fluxes
| $F_{1+}$ | 0.63     | 0.54         | 1.46         | 1.76         | 4.40   | 5.33     |
| $F_{1-}$ | 0.68     | 0.88         | 3.28         | 3.35         | 10.92  | 11.36    |
| $F_{1}$  | 0.13     | 0.31         | 1.02         | 0.99         | 3.10   | 1.94     |
| $F_{4+}$ | 2.13     | 2.08         | 6.86         | 5.30         | 6.92   | 7.64     |
| $F_{4}$  | 2.14     | 1.88         | 5.98         | 4.59         | 4.80   | 5.37     |

Table 1
Compartment sizes and fluxes. Observed and modelled compartment sizes [t ha$^{-1}$] and fluxes [t ha$^{-1}$ yr$^{-1}$] at ages 14 and 20 [years] under a control treatment (N-) and a fertilization/irrigation treatment (N+). Compartment sizes for $X_1$ (internal nitrogen) were estimated from a relationship in Madgwick et al. (1977) which averages over various environmental conditions. No direct observations were available on $F_{1+}$, $F_{1-}$, and $F_{2+}$. See text for details.
Swedish Coniferous Forest Project (SWECON). This project has been documented in detail (e.g., Persson, 1980); of particular interest for the present analysis are the reports by Ågren et al. (1980) and Linder and Axelsson (1982). Most of the relevant data were later summarized in an appealing graphical form by Cannell (1985, figs. 2A and 7). In addition to comparisons between the model results and these data on relatively young plantations, some results will be compared with observations on comparable, older stands within the SWECON project (Albrektson, 1980).

The data consist of biomass budgets, which are available for trees of age 14 (Ågren et al., 1980), as well as for fertilized/irrigated trees and a control group at age 20 (Linder and Axelsson, 1982). The budgets consist of measurements of major biomass compartments within trees and of fluxes into, out of, and between these compartments. The compartment sizes are expressed in units of t ha\(^{-1}\) and the fluxes in t ha\(^{-1}\) yr\(^{-1}\). These units can be converted to represent carbon content and carbon production, as is shown in the above-cited literature, but we shall refer exclusively to biomass.

Linder and Axelsson (1982) subdivide total tree biomass into current needles, current shoot axis, branches, stems, stumps, coarse roots and fine roots. However, the data on younger trees (Ågren et al., 1980) show less detail, and this fact has suggested that we restrict our analysis to three primary compartments, namely foliage, stems (including branches and stumps) and roots. The numerical values used for our analyses are included in Table 1, along with some of the modeling results. In the following we shall refer to the control and fertilization/irrigation treatments as N\(^{-}\) and N\(^{+}\), or we shall talk about phenomena at ages 14 and 20\(^{-}\) or 20\(^{+}\).

While the budgets are almost complete, the root biomass at age 14 is missing. A value of 0.8 for this compartment was derived through extrapolation. It turned out that the estimation of model parameters was rather insensitive to this value. Furthermore, the loss of foliage biomass through grazing and litterfall was not a part of these budgets. However, other analyses within the SWECON project (e.g., Persson, 1980, pp. 298, 451 and 572) suggest that, depending on age and other factors, between 15% and 30% of leaf biomass are lost every year.

We added to the three biomass compartments a compartment of internal nitrogen because of the prominent role nitrogen plays in the dynamics of the fertilized stand versus the control stand. While data on internal amounts of nitrogen were not available for the above trees, estimates were obtained from an analysis of above ground dry matter and nutrients in pines by Madgwick et al. (1977). Their fig. 10 shows nitrogen content, plotted against dry weight, for several pine species. Madgwick and coworkers also computed a functional relationship between the two variables through multiple regression in logarithmic coordinates, along with a specific correction term for *P. sylvestris*. From their results and the known above ground biomasses at ages 14, 20\(^{-}\) and 20\(^{+}\), we deduced nitrogen contents for the three stands of interest; these are given in Table 1.

It is noted that these results on nitrogen content are consistent with data on sapwood increments in the investigated stands (Linder and Axelsson, 1982, fig. 1) and the common assumption that the amounts of available nitrogen are proportional to increments in sapwood (e.g., Ågren and Ingestad, 1987 and refs. therein), as the following computation suggests. For the unfertilized control group, the sapwood increment in 20-year-old trees is about 2.75 times the increment at age 14, whereas in fertilized 20-year-old trees, the increment is about 6.7 times the increment at age 14. Estimating the initial amount of nitrogen in 14-year-old trees as 0.023 t ha\(^{-1}\), according to our analysis of the relationship in Madgwick et al. (1977), the amounts for the control and fertilized trees at age 20 would be 2.75 \times 0.023 t ha\(^{-1}\) = 0.063 t ha\(^{-1}\) and 6.7 \times 0.023 t ha\(^{-1}\) = 0.154 t ha\(^{-1}\). This is comparable with values directly computed from the relationship in Madgwick et al. (1977) (see also Table 1). It is noted that these are rough estimates since they average over different soil nutrient conditions, and since the scatter around the regression line is considerable. In fact, it turned out in our parameter estimation (see later) that the nitrogen levels predicted by our model are below the values
computed from the relationship in Madgwick et al. (1977) in the case of the unfertilized control treatment and that they exceed Madgwick's average values in the fertilized plantation.

These amounts of internal nitrogen are used in our modeling approach merely as three data points. No specific relationship between internal nitrogen and growth rate is assumed as a mathematical constraint, as has been done in other models (e.g., Ågren and Ingemad, 1987). In fact, we shall see later that the relationship predicted by the model is almost, but not strictly, linear.

3. Model

The rationale behind the proposed model for growth and biomass partitioning was discussed in the companion paper (Voit and Sands, 1996) as an example for how to develop a canonical model, and it suffices here to review the underlying definitions of variables and processes.

3.1. Variables

The first step of the canonical modeling procedure is the identification of relevant compartments and of the processes that connect them. The compartments in this case are dictated by the data, and we code them as

- \( X_1 \) = amount of internal nitrogen,
- \( X_2 \) = foliage biomass,
- \( X_3 \) = stemwood biomass (including stem, branches, and stump),
- \( X_4 \) = root biomass.

As an independent variable, we add
- \( X_5 \) = amount of available external nitrogen.

Independent variables affect the system but are not affected by the system. Numerically they could be lumped with parameter values, but it is often convenient to retain them separately from parameters to show explicitly how they affect the system. In contrast to the state variables, independent variables are not represented in the form of a differential equation, since they normally don't change during the experiment. Of course, scenarios can be simulated in which external factors change, as is the case with the daily and seasonal changes in solar radiation. Such inputs in the form of time series can be represented with piecewise solutions or the use of input modules (cf. Voit, 1993).

3.2. Processes

Focussing on a time scale of years we identified the following processes.

1. Nitrogen uptake is affected by the current internal and external nitrogen levels. It is also a function of the current root biomass and of the current foliage biomass which provides chemical energy.

2. Use of internal nitrogen is affected by all biomass compartments, each of which needs nitrogen for structure building and respiration.

3. Foliage growth is affected by the current foliage biomass and by the internal nitrogen level. Both are necessary for photosynthetic activity, and nitrogen is known to affect partitioning to foliage, stem, and roots.

4. Foliage loss is a function of the current foliage biomass. We explored the possibility that nitrogen would affect foliage loss since it contributes to respiratory processes. However, it turned out that this influence was negligible (cf. Section 4).

5. Stemwood growth depends on foliage biomass and on the available nitrogen level. The same arguments as in (3) apply.

6. Stemwood loss is a function of stemwood biomass. Again, potential effects of nitrogen turned out to be negligible.

7. Root growth is affected by the internal nitrogen level and foliage biomass. The same arguments as in (3) apply.

8. Root loss is a function of the internal nitrogen and the current root biomass.

In contrast to traditional models, the identification of processes in the canonical approach makes no assumptions about the mathematical form of the processes.

3.3. Equations

As shown in the companion paper (Voit and Sands, 1996), the model equations are developed
in a straightforward fashion from qualitative knowledge about the underlying processes. For instance, the dynamics of foliage consists of two components, \( F_2^+ \) and \( F_2^- \). One \( (F_2^+) \) includes all influences, factors, and controls that contribute to foliage biomass production, and the second component \( (F_2^-) \) includes all influences, factors, and controls that contribute to foliage loss. According to the previous identification of processes, \( F_2^+ \) is a function of the current foliage biomass \( (X_2) \) and the internal nitrogen level \( (X_1) \), whereas all other influences are collectively represented by the model’s parameters. In mathematical terms, \( F_2^+ \) is a function of \( X_1 \) and \( X_2 \), and in our canonical modeling approach, this function is a product of powers in \( X_1 \) and \( X_2 \):

\[
F_2^+ = \alpha_2 X_1^{g_21} X_2^{g_22}
\]  

The multiplier \( \alpha_2 \) represents the rate of the process and is positive by definition. The exponents \( g_{21} \) and \( g_{22} \) quantify the overall effects that \( X_1 \) and \( X_2 \) have on the production of foliage biomass, \( F_2^+ \). These parameters can be positive, negative or zero, depending on whether they represent positive, inhibiting, or negligible effects.

All production and utilization terms for the dynamics of each state variable are constructed in this manner. Based on our identification of relevant processes, the resulting S-system model is

**Internal nitrogen:**

\[
\dot{X}_1 = \alpha_1 X_1^{g_11} X_2^{g_12} X_3^{g_13} X_4^{g_14} - \beta_1 X_2^{h_12} X_3^{h_13} X_4^{h_14}
\]

**Foliage biomass:**

\[
\dot{X}_2 = \alpha_2 X_1^{g_21} X_2^{g_22} - \beta_2 X_1^{h_21} X_2^{h_22}
\]

**Stemwood biomass:**

\[
\dot{X}_3 = \alpha_3 X_1^{g_31} X_2^{g_32} - \beta_3 X_1^{h_31} X_3^{h_32}
\]

**Root biomass:**

\[
\dot{X}_4 = \alpha_4 X_1^{g_41} X_2^{g_42} - \beta_4 X_1^{h_41} X_4^{h_42}
\]

**External nitrogen:**

\[
X_5 = \text{independent}
\]

The model equations are thus established, and the next step is parameter estimation.

### 4. Parameter estimation

The data (Table 1) we use contain compartment sizes for foliage, stemwood, roots and almost all necessary biomass fluxes at age 14 and for two treatments \( (N^+ \text{ and } N^-) \) at age 20. These quantities correspond to values of the variables \( (X_i) \) and fluxes \( (F_i^+ \text{ and } F_i^-) \) at ages 14 and 20\(^+ \text{ or } 20^- \). A single set of parameter values has to model these three scenarios, the only difference between the fertilized and the control plantations being a different value for the independent variable \( X_5 \) which represents external nitrogen. If the parameter values would change between the ages of 14 and 20, they would be functions of time and thus variables, rather than parameters. Similarly, if the parameter values were different for the \( N^+ \text{ and } N^- \) treatments, they would be functions of the external or internal nitrogen concentrations \( X_5 \) and/or \( X_1 \) and, thus would have to be modeled as additional state variables.

The data thus provide values for most of the fluxes \( F_i^+ \text{ or } F_i^- \) at times 14 and 20\(^+ \text{ or } 20^- \), along with values of all variables at these points in time. As an example of the estimation procedure, we analyze foliage increment. Foliage increment is represented in the S-system model (2) as

\[
F_2^+ = \alpha_2 X_1^{g_21} X_2^{g_22}
\]

Taking logarithms on both sides transforms the equation into the linear equation

\[
\ln(F_2^+) = \ln(\alpha_2) + g_{21} \ln(X_1) + g_{22} \ln(X_2)
\]

and substituting the observed foliage sizes \( X_1 \) and \( X_2 \) and fluxes \( F_2^+ \) of the three data sets, we have a system of three linear equations in \( \ln(\alpha_2) \), \( g_{21} \) and \( g_{22} \). In principle, this system can be solved uniquely in all practically relevant cases. However, the variables and fluxes are subject to unknown measurement errors, and the estimated parameters turned out to be very sensitive to small variations in the \( X \)s and \( F \)s. If more data sets, of exactly the same nature as those used here, were available, the parameter estimation would reduce simply to multiple linear regression, as shown in the companion paper (Voit and Sands, 1996). However, this is not the case, and
we have to substitute this straightforward estimation with a customized ad hoc method.

Since the analytical solution with the measured compartment sizes and fluxes was found to be very sensitive, we computed families of solutions for numerous combinations of \( \ln(X) \pm \epsilon \) and \( \ln(F_{-}^+) \pm \epsilon \) that corresponded to different magnitudes of presumed measurement errors. Specifically, we allowed \( \epsilon \) variations in a range up to 10%. The result consists of families of parameter triplets \((\ln(a_{2}), g_{21}, g_{22})\) each of which satisfies the above linear equation for some \( \ln(X_1) \pm \epsilon_1, \ln(X_2) \pm \epsilon_2, \) and \( \ln(F_{-}^+) \pm \epsilon_3 \). These families turned out to lie in a close vicinity of straight lines.

Selection of the "best" solutions was done by hand (as described below), since a rigorous mathematical procedure would require simultaneous optimization of differential equations and algebraic flux equations, in addition to the establishment of balanced criteria of optimality, expressed in unambiguous mathematical terms. It is therefore likely that further adjustments within the given boundaries could slightly improve the fit to the particular data sets analyzed. However, considering that our analysis is based on a very small set of data, potential further improvements in fit appeared to be irrelevant. Future analyses will be more reliable if the experiments are repeated often enough to provide reasonable error estimates.

Instead of attempting the task of an exhaustive numerical optimization, we selected solutions and adjusted them according to the following guidelines of biological relevance: (1) While one has to acknowledge the possibility that the observational error may be of the order of 10%, the selected parameter values should keep the residual errors between model and data as small as possible. (2) Parameter estimates should make physiological sense. For example, flow of material must be represented by positive exponents and inhibitory effects by negative exponents; large magnitudes indicate strong effects, smaller magnitudes lesser effects. (3) Upon complete parameter estimation, the model for young trees should behave "naturally", with all biomasses initially increasing. (4) Parameter values very close to zero should be set equal to zero to reduce complexity; for instance, the influence of nitrogen on losses of foliage and stemwood turned out to be so small that we set \( h_{21} \) and \( h_{31} \) equal to zero.

While these guidelines were sufficient to determine parameter values for most fluxes, the ad hoc methods could not be used for \( F_{1}^{+}, F_{-}^{-}, \) and \( F_{-}^{-} \), since no experimental measurements of these fluxes were available. The parameters in the fluxes \( F_{1}^{+} \) and \( F_{-}^{-} \) were selected in a range that was found in many biochemical studies to correspond to traditional rate laws (e.g., cf. Shiraishi and Savageau, 1993). The model turned out to be quite insensitive to these values. The kinetic order in the flux \( F_{-}^{-} \), describing foliage loss, was chosen to describe a proportional loss \( (h_{22} = 1) \), whereas the rate was optimized within the observed range of 15% to 30% (e.g., Persson, 1980, pp. 298, 451 and 572).

Since only two treatments were compared, trends in fertilization effects could not be quantified, as can be seen from the following arguments. First, it is known that after 14 years of age one plantation was fertilized and irrigated while the control plantation continued to grow on untreated poor soil, but it is difficult to estimate how much nitrogen in an appropriate chemical and physical constitution was actually available to the trees. Second, the external nitrogen concentration enters only the first equation in the uptake term. It carries its own kinetic order \( (g_{15}) \) and contributes to the rate constant \( t_{1}^{l} \). Thus, the nitrogen concentration itself and two parameter values are unknown and their numerical values cannot be separated on the basis of the available data. This is readily seen when one chooses a different scale for \( X_{5} \). For instance, if we replace \( X_{5} \) with \( 100 \times X_{5} \), the difference in effect is absorbed during parameter estimation in the rate constant \( \alpha_{1} \), and the two models are mathematically identical. \( X_{5} \) could also be replaced with a power of \( X_{5} \), which could, for instance, reflect increased fertilization for larger trees, and again this alteration would be absorbed by the model, in this case through an adjustment in \( g_{15} \). Because of the intrinsic redundancies, we assigned a kinetic order of 1 and adjusted the values of \( \alpha_{1} \) and \( X_{5} \) accordingly. If further evidence becomes
available, the values of the kinetic order and the rate constant can be made more realistic.

As part of the estimation process, initial conditions at time \( t = 0 \) were obtained by extrapolating the model from \( t = 14 \) back to \( t = 0 \) and assuring monotonicity in biomass increases at young ages. This requirement eliminated some otherwise admissible families of parameter values. Within a reasonable range, the initial values for \( X_1 \) and \( X_2 \) turned out to have a minor impact on the numerical results, and the initial values for \( X_3 \) and \( X_4 \) were almost irrelevant.

The parameter estimation procedure resulted in the following S-system model.

Internal nitrogen:

\[
\dot{X}_1 = 9.5 \times 10^{-5} X_1^{-1} X_2^{0.72} X_4^{0.72} X_5 \\
- 6.5 \times 10^{-5} X_2 X_3 X_4 \\
X_1(0) = 0.0015
\]

Foliage biomass:

\[
\dot{X}_2 = 3.2 X_1^{0.5} X_2^{0.57} - 0.2 X_2 \\
X_2(0) = 0.03
\]

Stemwood biomass:

\[
\dot{X}_3 = 5 X_1^{0.5} X_2^{0.7} - 0.2 X_3^{0.7} \\
X_3(0) = 0.01
\]

Root biomass:

\[
\dot{X}_4 = 0.36 X_1^{-0.4} X_2 - 0.75 X_1^{-0.3} X_4^{0.8} \\
X_4(0) = 0.01
\]

External nitrogen:

\[
X_5 = 1 \text{ (N}^{-}\text{ treatment; N}^{+}\text{ treatment, prior to age 14)} \\
X_5 = 9 \text{ (N}^{+}\text{ treatment, beginning at age 14)}
\]

The loss term for foliage, \( F_2 \), indicates a yearly loss of 20\%. This percentage seems to be appropriate for foliage in \textit{Pinus sylvestris} (e.g., Persson, 1980, pp. 298, 451 and 572). While the same rate constant was found for stemwood (cf. \( \beta_3 = 0.2 \) in the loss term \( F_3 \)), the kinetic order in this case, \( h_{33} \), had to be smaller to fit the data. This means that the relative loss of stemwood decreases with age because \( X_3 \) increases with time. It may reflect that older trees shed branches as canopy rises and that in older trees much of the biomass is tied up in heartwood which does not respire. Also, respiration is often considered to be proportional to stem area rather than volume, which again suggests a kinetic order of less than 1.

As discussed above, the numerical values of \( X_5 \) at this point are almost meaningless. More fertilization treatments are required to characterize the effect of \( X_5 \) more precisely.

5. Results

The results are based on solving this system (5) numerically. This solution can be obtained with any numerical integrator, but it is most efficient to use the interactive software ESSYNS (Voit et al., 1990) which was custom made for the evaluation of S-systems and allows the user to explore S-system models with single keystroke commands and without compiling. To compare the model results with the original data, we solved the system from \( t = 0 \) to \( t = 14 \) with \( X_5 = 1 \) (N\(^-\) treatment). We then extended the solution up to \( t = 20 \) either continuing the nitrogen poor N\(^-\) treatment \((X_5 = 1)\) or modeling fertilization \((N^+; X_5 = 9)\). For explorations of the effects of external nitrogen, we solved the system from \( t = 0 \) toward desired ages with different values of the external nitrogen variable \( X_5 \). For ages beyond 20 years, we assumed continuation of the fertilization scheme at ages 14 to 20: The control group was assumed to continue growing on poor soil, whereas the treatment group was assumed to receive yearly fertilization.

5.1. Integration of data

Table 1 shows a comparison of observed and modeled biomasses and fluxes and indicates that the model reproduces all compartment sizes and most of the fluxes within a margin of relative error that is to be expected in the type of data we analyze. The relatively larger discrepancies in fluxes are not surprising, since flux measurements are subject to greater uncertainties than assessments of biomasses. The good correspondence
between model and data provides strong support for the validity of the model structure since the input to the model did not consist of time series data to which the model was fitted with some conventional least-squares regression scheme. Instead, the input consisted of overall qualitative knowledge about biomass flow which was integrated in the canonical model (2) and then quantified through power-law representation of individual fluxes, based on point observations from the three scenarios.

The correspondence between model output and observed data as given in Table 1 is not an automatic consequence of the process of parameter estimation. The technique by which parameters are estimated guarantees that if a solution of the differential equations (5) passes through a set of observed \( X_i \) at any one of the times 14, 20\(^+\) and 20\(^-\), then the corresponding fluxes \( F_i^+ \) and \( F_i^- \) must be close to the observed values. However, it does not guarantee that there exists a solution which simultaneously passes through the observed \( X_i \) at all three times 14, 20\(^+\) and 20\(^-\). For this to be the case both the structure of the model and the values of its parameters must be consistent with the observed data. Consider for the moment the conventional technique for estimating parameters in a model, in which a nonlin-

Fig. 1. Annual changes in biomass [t ha\(^{-1}\)] and internal nitrogen concentration (%) under control (N\(^-\)) or fertilizer (N\(^+\)) treatment: (a): foliage biomass, \( X_2 \); (b): root biomass, \( X_4 \); (c): stemwood biomass, \( X_3 \), for the original model (solid lines) and the alternate model (dotted lines); (d): internal nitrogen concentration, \( X_1 \).
A least-squares technique is applied to determine a set of parameter values which minimizes the sum of squared differences between predicted and observed $X_i$ at times $14$, $20^+$ and $20^-$. While this process provides a set of parameters which guarantee the model will reproduce the observed $X_i$, within some error, it does not guarantee it will reproduce the observed fluxes $F_i^+$ and $F_i^-$. Again, this will only be the case if the model has the appropriate structure. Finally, it is noted that parameter estimation is usually based on fitting results from the model only to observed state variables, their rates of change being ignored, or often unobserved. In our case, the estimation technique is based on both state variables and individual components of their rates of change, i.e. the influxes $F_i^+$ and effluxes $F_i^-$. This is a much more stringent process than conventional parameter estimation. These considerations suggest that the agreement shown in Table 1 between model and experiment provides strong support that both the model structure and its parameters are consistent with the observed data.

5.2. Growth dynamics

An important test for the validity of the model is its prediction of growth patterns beyond the observed 20 years of age. These patterns are obtainable when one integrates the differential equations (5) over a longer period of time. The resulting functions of biomasses versus time exhibit definite trends, indicating that stemwood increases in a more or less sigmoidal fashion, while foliage and root biomasses show a clear "overshoot", i.e., reach a temporary maximum before they decrease to their final sizes (Fig. 1a–c). No definite data beyond age 20 are available for comparison with these model predictions, but the predicted dynamics follows empirical observations in other pine stands of the SWECON project (e.g., Albrektson, 1980). The predictions also are "in agreement with general silvicultural understanding" (Mäkelä and Hari, 1986), and considered a proper outcome in other theoretical studies (e.g., West, 1987, 1993).

The timing of the overshoots in leaf and root biomasses depends on the external nitrogen conditions and occurs between about 20 and 30 years. This time period is consistent with Albrektson’s observations on pines (Albrektson’s fig. 2) and with the results of other types of simulation studies (e.g., Mäkelä and Hari, 1986; West, 1987, 1993). While the stands under study have not yet reached their final ages, general quantitative trends in biomass dynamics in $P. sylvestris$ can be extracted from fig. 2 and table 3 in Albrektson (1980), which provide biomasses of different tree compartments in various types of plantations. Solving our model for the two fertilizer treatments up to 80 years, by when foliage and roots have about reached their final sizes, we obtain foliage biomasses of 7 and 12 t ha$^{-1}$, coarse root biomasses of 6 and 14 t ha$^{-1}$, and stemwood of about 35 and 105 t ha$^{-1}$, respectively (Fig. 1a–c). These results are quantitatively consistent with Albrektson’s data. However, the numerical values have to be considered with caution, because they are based on merely three biomass budgets for relatively young trees. For instance, if the parameter values of the stemwood dynamics in (5) are slightly altered ($g_{32} = 0.57$, $\beta_3 = 0.3$, $h_{33} = 0.5$), the compartment sizes and fluxes related to $X_3$ change moderately, but the long-term stemwood development differs noticeably from the previous case (Fig. 1c: dotted lines). The other variables are only marginally affected (data not shown).

While the amount of internal nitrogen, $X_1$, is growing with age and with external nitrogen availability ($X_3$), the internal nitrogen concentration decreases with age (Fig. 1d), since the biomass pools grow faster than the internal nitrogen pool. This decrease in concentration is consistent with the fact that the functional relationship between nitrogen content and dry matter is concave (Madgwick et al., 1977). It is also indirectly supported by Madgwick's observation that the nitrogen concentration in wood is much smaller than in branches and bark, which results in lower overall nitrogen concentrations when the proportion of wood increases. Decreases in nitrogen concentration with age have also been observed in other species (e.g., Frederick et al., 1985; Miller, 1989 and references therein).

Quantitative information about the changes in nitrogen uptake over the lifetime of a tree is not
Fig. 2. Examples of the dynamics of influxes as functions of tree age. (a): nitrogen uptake, $F^+_1$, [t ha$^{-1}$ yr$^{-1}$]; (b): ratio of stemwood production to foliage production.

Fig. 3. Quasi-allometric relationships between biomasses and biomass production [t ha$^{-1}$, t ha$^{-1}$ yr$^{-1}$]. (a): relationships between foliage ($X_2$), stemwood ($X_3$) and root ($X_4$) biomasses; (b): relationship between foliage biomass and sapwood area, represented as $X_3^{2/3}$; (c): relationship between foliage production and stemwood production; (d): relationship between foliage biomass and stemwood production. The dotted lines, indicating ages 2 and 20, enclose the approximate time period between stand establishment and canopy closure. See text for further comments.
readily available. An exception is Miller (1989) who reports a temporal uptake function that increases quasi exponentially over the first few years of growth, then reaches a maximum between ten and twenty years of age, and finally drops back to a lower level. Our model predicts the same pattern (Fig. 2a).

Fig. 5 in Albrektson (1980) indicates a saturating or overshooting relationship between tree height and the ratio of stemwood production over foliage production. Tree height is not a part of our model but increases monotonically with time. If we plot the corresponding ratio, \( F_3^+ / F_2^+ \), against time, we obtain the same pattern of overshoot and saturation (Fig. 2b).

5.3. Relationships between biomasses

Allometric relationships between stemwood, roots, and foliage have been observed many times (e.g., Pearsall, 1927; Cromer and Jarvis, 1989; Sands et al., 1992). They correspond to linear relationships on a logarithmic scale. Fig. 3a shows that indeed \( \ln(X_3) \) and \( \ln(X_4) \) are almost linearly related to \( \ln(X_2) \) during the tree’s growth phase, as indicated by dotted lines, but after canopy closure, the allometric relationship to stemwood biomass does not hold. This dynamic behavior is to be expected and is a necessary consequence of the fact that foliage and root biomasses reach a plateau while stemwood biomass continues to grow. The curl in the relationship between \( \ln(X_2) \) and \( \ln(X_4) \) is because \( X_2 \) overshoots slightly earlier than \( X_4 \).

Fig. 6 in Albrektson (1980) depicts foliage biomass in relation to sapwood area. The shown trend is locally linear but overall slightly curved in a concave fashion. Sapwood area is not a variable in our model, but if we assume that, at least until canopy closure, sapwood area is roughly an allometric function of stemwood biomass, with a power of 2/3, we can mimic Albrektson’s graph by plotting \( X_2 \) against \( X_5^{2/3} \). This plot (Fig. 3b) is almost linear until canopy closure. The same relationship is implicit in the allometric relationship between \( X_3 \) and \( X_2 \): If \( \ln(X_2) \) is plotted against \( \ln(X_3) \) (which corresponds to switching axes in Fig. 3a), the slope is about 2/3.

5.4. Relationships between production and biomasses

Fig. 3 in Albrektson (1980) indicates that foliage production over short periods of time is proportional to stemwood production, while depicted over the entire range the relationship exhibits a slightly concave trend. The corresponding result in our analysis, a plot of \( F_2^+ \) versus \( F_3^+ \), confirms these observations (Fig. 3c). In addition, our plot shows a returning trajectory at high production levels, which is a mathematically necessary consequence of the observed overshoot in foliage production. Fig. 4 in Albrektson (1980) shows a locally linear and overall slightly concave relationship between foliage biomass and stemwood production. A plot of \( X_2 \) versus \( F_3^+ \) has the same appearance (Fig. 3d).

Miller (1989) and other authors cited therein have observed a close to linear relationship between nitrogen uptake and primary production, when these processes are plotted in logarithmic coordinates. Again, the corresponding plot of \( \ln(F_2^+) \) versus \( \ln(F_2^+ + F_3^+ + F_4^+) \) in our model is very close to a straight line until canopy closes (not shown).

5.5. Effects of nitrogen on growth rate

Effects of external nitrogen are studied with our model by solving the differential equations from \( t = 0 \) to \( t = 80 \) with a particular value for the independent variable \( X_5 \). The untreated control group is simulated with the value \( X_5 = 1 \), and the fertilizer regimen specified by Linder and Axelsson (1982) with \( X_5 = 9 \). Values in between correspond to different degrees of partial fertilization. As an example, one may plot the allometric relationships between foliage, stemwood, and root for different values of \( X_5 \), and the results, similar to Fig. 3a, are consistent with data in Cromer and Jarvis (1989) and Sands et al. (1992): The allometric relationships between foliage and stemwood, computed under different nitrogen treatments, are almost identical, whereas the relationships between root and foliage biomasses have the same slope but an intercept that de-
creases with increasing nitrogen availability (not shown).

Ågren and Ingestad (1987 and references therein) have postulated a linear relationship between growth rate and the internal amount of nitrogen. By adding the right-hand sides of the model equations in (5) for foliage, stemwood, and roots, we obtain a measure of the tree's overall net growth rate at a given time. When we plot this growth rate, $X_2 + X_3 + X_4$, before canopy closure against the amount of internal nitrogen (Fig. 4a shows this relationship for age 10), the result is nearly linear over the full range from poor soil to the Linder and Axelsson (1982) regimen of full fertilization and irrigation. This is remarkable since the model itself is highly nonlinear and does not use any constraint equations that would enforce the direct proportionality between growth rate and nitrogen content.

5.6. Functional balance

Davidson (1969) postulated that, under varying environmental conditions, root and shoot activities were strictly coordinated. Many authors subsequently used this concept as the basis for modeling biomass partitioning in plants. Formally, the idea of Carbon and Nitrogen Balance was expressed as

$$\text{root mass} \times \text{rate of absorption} \propto \text{leaf mass} \times \text{rate of photosynthesis}$$

where “rate of absorption” and “rate of photosynthesis” are defined as “absorption per unit root biomass” and “photosynthetic activity per unit foliage biomass”. The corresponding balance in our model is thus

$$X_4 \times F_1^+ / X_4 \propto X_2 \times (F_2^+ + F_3^+ + F_4^+) / X_2$$

which is equivalent with

$$F_1^+ \propto F_2^+ + F_3^+ + F_4^+. \quad (7)$$

Indeed, the plot of $F_2^+ + F_3^+ + F_4^+$ against $F_1^+$ at age 10 is virtually linear for all reasonable nitrogen levels (Fig. 4b), and, for all practical purposes, supports Davidson’s hypothesis. It is emphasized again, that this result constitutes an output of the model and was not used in any way as an input or a constraint.

5.7. Biomass partitioning

It has been observed in some cases, and hypothesized in others, that the partitioning of biomass production to roots and other tissues is a function of nitrogen availability, and that more photosynthate is channeled into root growth under nitrogen poor conditions (e.g., Cannell, 1985; McDonald et al., 1986). Many models have postulated constant partition coefficients (e.g., McMurtrie and Wolf, 1983), used relationships consistent with the pipe theory of Shinozaki et al. (1964) or with Davidson’s hypothesis of functional balance (cf. Mäkelä, 1986; Mäkelä and

![Fig. 4](image-url)
Sievanen, 1987), or defined ad hoc functions of some of the state variables (e.g., Reynolds and Thornley, 1982; Johnson and Thornley, 1987). In contrast to these strategies, partitioning in the present model is strictly an output which is given as the ratios \( \eta_F = \frac{F_2^+}{F_2^+ + F_3^+ + F_4^+} \), \( \eta_S = \frac{F_3^+}{F_2^+ + F_3^+ + F_4^+} \), and \( \eta_R = \frac{F_4^+}{F_2^+ + F_3^+ + F_4^+} \), for foliage, stemwood, and roots, respectively.

Fig. 5a and b show, for the two treatments N− and N+, that the partitioning “coefficients” in fact are functions of time. They are not even monotonic functions, since they are affected at slightly different times by the overshoots in foliage and root biomass. In response to fertilization at age 14 (Fig. 5b), the allocation pattern shifts immediately from roots to an increased allocation to leaves and to an even more pronounced allocation to stemwood. The allocation pattern then stabilizes toward an allocation to foliage that is very close to that in the unfertilized control group, but with a slightly higher allocation to stemwood and a lower allocation to roots.

The model also allows us to analyze biomass

![Graphs showing biomass partitioning](image-url)
partitioning as a function of nitrogen availability at a fixed age. At age \( t = 10 \), for example, allocation to roots decreases with increasing availability of nitrogen, while allocation to foliage and stems increases with increased nitrogen levels (Fig. 5c). The same trend is found at ages 30 and older. However, the trends between the ages of 10 and 30 are not so simple. For instance, a tree at age 18 responds to very low nitrogen availability with high allocation to roots, an increase in nitrogen leads to more allocation to above ground compartments, and further increases shift the allocation pattern back toward the roots (Fig. 5d).

The intuitive explanation of a "proper partitioning strategy" is that, at low nitrogen levels, the tree increases root tissue in order to facilitate the increased uptake of external nitrogen. The second priority is an increase in foliage, since foliage contains the photosynthetic machinery that allows further growth of all compartments. Allocation to stemwood at times of low nitrogen availability is reduced to produce just enough stem material to support the growing foliage, whereas at high levels of available nitrogen, the tree can "afford" to allocate more biomass to wood production. The model results provide some fine tuning of these basic ideas by demonstrating that the allocation patterns are simultaneous functions of both nitrogen availability and age (Figs. 5 and 6). For rather young and rather old trees, the simple monotonic trend is confirmed by the model. However, toward the end of the rapid growth phase and during canopy closure, the model trees exhibit the more complicated patterns of responses to different nitrogen levels shown in the middle part of Fig. 6.

It must be emphasized that these "strategic" considerations constitute a mere interpretation of output results and were not used as design principles or constraints in the development of the model. Our modeling approach, thus, is fully consistent with the Cheeseman (1993) notion that plants have only local information and no means of devising anticipatory, global strategies.

6. Discussion

The data sets analyzed in this paper were sufficient to construct a canonical model and estimate its parameter values with only minor additional assumptions. Ideally, more data sets of the same type would have been available, as these would have simplified parameter estimation and allowed us to perform an assessment of the quality of data. Such additional data sets would have allowed us to compute the parameter values from biomasses and fluxes through simple linear regression instead of the manual perturbation technique we used. Nonetheless, even on the basis of a bare minimum of data, we were able to identify a model that shows a remarkable degree of internal and external consistency.

The results of the analysis are far from trivial. With inputs only from three relatively young stands, we were able to predict the further development of the stands up to old ages. While there were no corresponding data about these particular stands, all model predictions turned out to be consistent with "general observations" on sizes of compartments, on the relationships between compartments, and on relationships between various types of production and biomasses. In many cases these relationships "automatically" appeared as almost straight lines, confirming observations and constraints of proportionality presupposed in

![Fig. 6. Simultaneous dependence of biomass partitioning on age and nitrogen availability. Shown here is the allocation of biomass to compartments above ground. Allocation to roots is given as the complement of this surface (1 - above-ground allocation).](image-url)
other models, even though none of these relationships had been used to construct our highly nonlinear model. At the extremes, the model results showed deviations from linearity, for instance in the allometric relationships between biomasses, but these deviations are mathematical necessities of the observations themselves. For example, if one accepts that the biomass of leaves reaches an upper limit, whereas stemwood continues to increase, the allometric relationship between these two quantities must leave the straight line for large sizes and become horizontal or vertical, depending on how the plot is drawn.

The model reflected, also “automatically”, the well-accepted hypothesis of functional balance between roots and shoots. While again not strictly linear, the results over the relevant domains of parameter values produced lines that would readily be identified as “perfectly linear” had they been measured experimentally.

The model generated partitioning functions showing how much biomass is allocated to which tree parts, in dependence on age and fertilization. In contrast to the assumption of constant allocation coefficients or simple allocation functions employed in other models, our model revealed quite complex allocation patterns that seem to partition the produced biomass in response to the present combination of growth demands and nitrogen availability. While the results are intuitively reasonable, there seem to be no hard data yet to validate or contradict the model predictions.

There are many open questions that cannot be addressed with this model. For instance, monthly variations in biomasses are simply not detectable in our model since the model is based on the coarser time scale of years. Similarly, it is well known that partitioning changes during the course of a season (e.g., Cannell, 1985, fig. 8; Cannell et al., 1988, figs. 1, 2). Given corresponding data of monthly or bi-weekly budgets, we can see no reason in principle why a canonical model should not be able to model finer variations in biomass distributions and allocation patterns. However, the present model is too coarse for such analyses.

Important factors like temperature and water availability are not explicitly included in the model, but their effects are implicitly reflected in the measured biomass budgets. Again, as appropriate data become available, a canonical model accounting explicitly for the impact of water and temperature could be constructed.

The literature exhibits a large range in complexity in the uptake functions for external nitrogen (cf. Discussion in Voit and Sands, 1995). Our model does not contribute much to answering questions about uptake mechanisms as such, since data on only two scenarios with different external nitrogen levels are available. In the current model, we arbitrarily assigned a power of 1 to the external variable $X_5$ in the first equation. Since $X_5$ is a constant, it is obvious that this power could be replaced with any other non-zero power and that the difference could be made up by adjusting $\alpha_1$. If we had further biomass budgets, obtained under different nitrogen conditions, the effects of nitrogen availability on nitrogen uptake could be quantified; i.e., the kinetic order parameter $g_{15}$ could be identified. Our present simulations merely suggest that reasonable increases in $X_5$ lead to higher values of internal nitrogen, to greater biomasses, and to increased amplitudes in overshoots in the foliage and root dynamics.

It is possible that numerous data sets of the type amenable to this canonical approach are available in the forestry community but that they have never been published because of perceived deficiencies due to uncertainties or the lack of controls. Maybe this analysis will encourage colleagues to come forward with such data or to produce them with a canonical analysis in mind.

Acknowledgements

The authors like to express their gratitude to Dr. Philip W. West for his encouragement and for numerous discussions and suggestions. EOV is very grateful for the hospitality and for the financial support received from the Cooperative Research Centre for Temperate Hardwood Forestry during his sabbatical. This work was also supported in part by grants from Honeywell Technology Center, Minnesota; the USDA For-
est Service, Southeastern Forest Experiment Station, Charleston, SC; and the U.S. Department of Energy (DE-FG01-92EWS06).

References


References


